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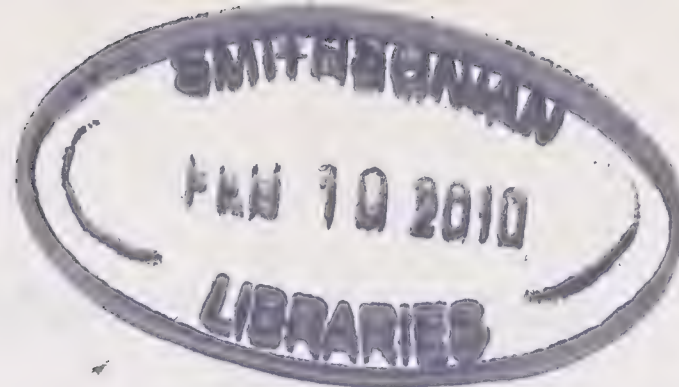
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ANATOMICAL RE-DESCRIPTION OF THE TERRESTRIAL ONCHIDIID SLUG *SEMPERONCIS MONTANA* (PLATE, 1893)

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ABSTRACT

Onchidiidae, one of the higher clades of pulmonates, have been understudied for the last 70 years; its systematics is in a state of confusion; and the internal anatomy of most species is still largely unknown. The anatomy of *Semperoncis montana*, a terrestrial species that lives in high-elevation rain forests of the Philippines Islands, is redescribed based on 91 specimens representing ten populations. New geographic records (Panay Island) and elevation records (up to 1,850 m) are provided. All type material available was re-examined. The intra-specific variation of anatomical characters is analyzed, with special attention to the radula and the male reproductive organs. Male organs (penial stalk and hooks, papillae and spines of accessory glands) are illustrated using scanning electron microscopy for the first time in onchidiids. Ontogenetic changes in the shape of male organs are described and illustrated in detail, indicating that *S. montana* was described based on immature specimens of the later named *Platevindex apoikistes*. Therefore, this latter name is regarded as a junior synonym of *S. montana*. The supra-specific relationships of *S. montana* are commented upon.

Key words: Euthyneura, intra-specific variation, Gastropoda, Philippines, Pulmonata.

INTRODUCTION

Onchidiidae, one of the higher clades of pulmonates, is poorly known, mainly because it has been understudied for the last 70 years and because its systematics has never been revised (Dayrat, 2009). The nomenclatural status of most species names is unknown and onchidiid species diversity is in state of confusion; whether Labbé's (1934) 14 genera refer to monophyletic, paraphyletic, or polyphyletic taxa is unknown; and higher relationships within onchidiids are also unknown. Finally, as Britton (1984) pointed out, virtually nothing is known about the individual variation of the characters used in onchidiid systematics; anatomical knowledge of onchidiids is also poor, the internal anatomy of the vast majority of the species still being unknown. Information on the general morphology of onchidiids, including the terminology traditionally used – such as dorsal eyes, peripodial groove, marginal glands – can be found in Dayrat (2009, and references therein).

Most onchidiid slugs are marine and live in the upper tidal zone, either in rocky, sandy, or muddy habitats, including mangroves. However, two species have been described from

brackish habitats and tolerate fresh water: *Onchidium typhae* Buchannan, 1800, and *Labella ajuthiae* (Labbé, 1935). Also, three terrestrial species have been described from high-elevation rainforests: *Semperoncis montana* (Plate, 1893), known from only the three syntypes collected on land (at an unknown elevation) from Sibugan Island, Philippines; *Platevindex ponsonbyi* (Collinge, 1901), known from only the holotype collected at 850–1,060 m from Borneo; and, *Platevindex apoikistes* Tillier, 1983, known from 38 specimens collected from the eastern slope of Mt. Halcon, Mindoro Island, Philippines, at 400–600 m.

The main goal of the present study is to re-evaluate the species diversity of terrestrial onchidiids, that is, more specifically, to determine how many species live on land in the Philippines Islands. It is based on the examination of type material available (*Semperoncis montana* and *Platevindex apoikistes*), as well as 36 new specimens collected from Panay (150–1,850 m) and 14 new specimens from Mindoro (1,200–1,550 m) islands, which represent new geographical (Panay) and elevation records (highest elevation of terrestrial onchidiids previously known was 1,060 m, which is now 1,850 m). Unfortunately, at this stage,

the case of *Platevindex ponsonbyi* must be left aside because its type material could not be found, its original description is too short, and no additional material is available (see Discussion).

The present detailed analysis of individual variation suggests that all specimens examined here are members of the same species. Differences previously mentioned between *apoikistes* and *montana* were due to the fact that these two species were described based on sexually mature and immature individuals, respectively. Ontogenetic changes of two key organs for taxonomy – penial apparatus and male accessory gland – are described in detail.

MATERIALS AND METHODS

Material Preparations

In total, 91 specimens were examined for the present study, including 41 types: 38 types (one holotype and 37 paratypes) of *apoikistes*, three syntypes of *montana*, and 50 new, additional specimens. All specimens are deposited in museums: Florida Museum of Natural History, Gainesville (FLMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), and the Naturmuseum Senckenberg, Frankfurt am Main (SMF). The holotype and two paratypes of *apoikistes* were already dissected by Tillier (1983); four additional paratypes were dissected for the present study; the other paratypes were examined externally but not dissected. One syntype of *montana*, dissected prior to the present study, was examined again, including its reproductive organs; the two other syntypes were only examined externally. Finally, out of the 50 new specimens, 27 were dissected and 23 were examined externally.

For the 32 specimens dissected, both the external morphology and the internal anatomy were observed. All anatomical observations were made under a dissecting microscope and drawn with a *camera lucida*. In addition, organs were prepared for scanning electron microscopy (SEM) for most specimens dissected.

Radulae were cleaned in 10% NaOH for a week, rinsed in distilled water for at least a week, briefly cleaned in an ultrasonic water-bath (less than a minute), sputter-coated with gold-palladium, and examined by SEM (UCM SEM-laboratory). Soft parts (penis, penial gland, etc.) were dehydrated in ethanol and critical point dried before coating. In total, 30

SEM stubs were prepared. When a lot included several specimens, each specimen was labeled, both inside the jar and on the stubs, so that future workers will be able to link unambiguously the present anatomical descriptions to particular individuals in museum collections. All SEM stubs prepared for the present study will be sent back with the specimens to the museum collections.

Anatomical Abbreviations

ag	accessory gland
alg	albumen gland
dd	deferent duct
dg	digestive gland
e	esophagus
hd	hermaphroditic duct
hg	hermaphroditic gland
i	intestine
lcg	left cerebral ganglion
rpg	right pleural ganglion
mg	mucous gland
ov	oviduct
pa	papilla (accessory gland)
ps	penial sheath
rcg	right cerebral ganglion
rg	rectal gland
rps	reproductive system
sp	spermatheca
spv	spermoviduct
st	stomach
vg	visceral ganglion

ANATOMICAL RE-DESCRIPTION

Semperoncis Starobogatov, 1976

The type species, by subsequent designation (Starobogatov, 1976: 211): *Semperoncis glabra* (Semper, 1885), *Semperoncis* being a replacement name for *Semperella* Labbé, 1934, *non Semperella* Gray, 1868 (Porifera).

Semperoncis montana (Plate, 1893) (Figs. 1–75)

Oncis montana Plate, 1893: 194–196, pl. 7, figs. 3, 23; pl. 11, figs. 57, 58, 71; pl. 12, fig. 89. – Hoffmann, 1928: 87–88.

Semperella montana – Labbé, 1934: 236.

Platevindex montana – Tillier, 1983: 198–202, fig. 3.

Platevindex apoikistes Tillier, 1983: 198–202, figs. 1, 2, 4–7, **new synonym**.

Type Material

Three syntypes of *Oncis montana* (SMF 256164): three specimens 18/17 (#1), 15/13 (#2), and 15/15 (#3) mm preserved, leg. Dr. von Möllendorf, [collecting date unknown]. The syntypes of *montana* are in very poor condition as they likely remained dry for a while before being put back in alcohol. As a consequence, they are very rigid and dark brown.

Holotype of *Platevindex apoikistes* (MNHN, no catalogue number): one specimen 40/31 mm preserved, leg. Philippe Bouchet, December 1980; 37 paratypes of *Platevindex apoikistes* (MNHN, no catalogue number): four specimens dissected 35/25 (#1), 23/14 (#2), 42/26 (#3) and 26/14 (#4) mm preserved [other paratypes were not dissected; spm #2 is the smallest paratype, and spm #3 is the largest]. The type material of *apoikistes* is well preserved, both externally and internally; the holotype was entirely dissected and cut in pieces by Tillier for the original description.

Type Localities

Oncis montana: Philippines, Sibuyan Sea [Sibuyan Island, on land, unknown altitude]. *Platevindex apoikistes*: E slope of Mt. Halcon, Mindoro oriental [Mindoro Island], 400–600 m altitude.

Additional Material Dissected

Philippines, Panay Island, Antique Province, western ridge of Mt. Madja-as, 1,100 m, 6 April 1992, 13 specimens 20/12 (#1), 33/18 (#2), 19/15 (#3), 21/14 (#4), 23/11 (#5) and 32/21 (#6) mm preserved [seven additional specimens were not dissected; spms #1 and #3 are the smallest, and spm #2 is the largest], leg. K. Auffenberg et al., identified as *Onchidium*, [identifier unknown], (FLMNH 245117); Philippines, Panay Island, Antique Province, just below peak Mt. Madja-as, 1,850 m, 8 April 1992, two specimens 28/20 (#1) and 34/19 (#2) mm preserved, leg. PNM staff, identified as *Onchidium*, [identifier unknown], (FLMNH 245142); Philippines, Panay Island, Antique Province, western ridge of Mt. Madja-as, 900 m, 11 April 1992, 14 specimens 32/20 (#1), 25/15 (#2), 23/17 (#3), 32/20 (#4), 28/17 (#5) mm preserved [nine additional specimens were not dissected; spm #2 is the smallest, and spms #1 and #4 are the largest], leg. K. Auffenberg et al., identified as *Onchidium*, [identifier un-

known], (FLMNH 245191); Philippines, Panay Island, Capiz Province, 3.0 km NE of Pilar, 150 m, 11°25'24"N, 120°57'44"E, 26 April 1992, 2 specimens 25/19 (#1) and 25/15 (#2) mm preserved, leg. K. Auffenberg et al., identified as *Onchidium*, [identifier unknown], (FLMNH 245549); Philippines, Panay Island, Aklan Province, NE of Mt. Madja-as, 1,430 m, April 1992, 5 specimens 14/9 (#1), 18/12 (#2), 14/10 (#3), 16/9 (#4) and 17/13 (#5) mm preserved, leg. L. Ruedas et al., identified as *Onchidium*, [identifier unknown], (FLMNH 245797).

Philippines, Mindoro Island, Baco Municipality, Mount Halcon, Hanglo, 1,550 m, 4–8 June 1992, one specimen 28/19 mm preserved, leg. Rafe Brown, identified as *Onchidium*, [identifier unknown], (FLMNH 245788); Philippines, Mindoro Island, Mindoro Oriental Province, Baco Municipality, Mount Halcon, N ridge, Dulangan River valley, 1,200 m, 13°17'27"N, 120°59'32"E 27 May 1992, four specimens 26/18 (#1), 23/17 (#2) and 24/23 (#3) mm preserved [a fourth spm 26/22 mm was not dissected], leg. Rafe Brown, identified as *Onchidium*, [identifier unknown], (FLMNH 245776); Philippines, Mindoro Island, Mindoro Oriental Province, Baco Municipality, Mount Halcon, N ridge, Dulangan River valley, 1,200 m, 13°17'27"N, 120°59'32"E, 28 May 1992, nine specimens 35/23 (#1), 25/20 (#2) and 32/28 (#3) mm preserved [six additional specimens were not dissected; spm #1 is the largest, and spm #2 is the smallest], leg. Rafe Brown, identified as *Onchidium*, [identifier unknown], (FLMNH 245777).

Distribution

Philippines: Sibuyan Island (type locality of *montana*); Panay Island (present study); Mindoro (type locality of *apoikistes*; present study). Note that Hoffmann (1928) and Labbé (1934) cited Plate's (1893) work but did not add new material or data.

From 150 to 1,850 m: 150 m (Panay Isl.), 400–600 m (Mindoro, original description of *apoikistes*), 900 m (Panay Isl.), 1,100 m (Panay Isl.), 1,200 m (Mindoro Isl.), 1,430 m (Panay Isl.), 1,550 m (Mindoro Isl.), 1,850 m (Panay Isl.).

Color (Figs. 1–7)

No information is available on the color of live animals. Dorsal preserved color from light brown mottled with darker areas to homogeneous dark bluish black. Individuals with a dark



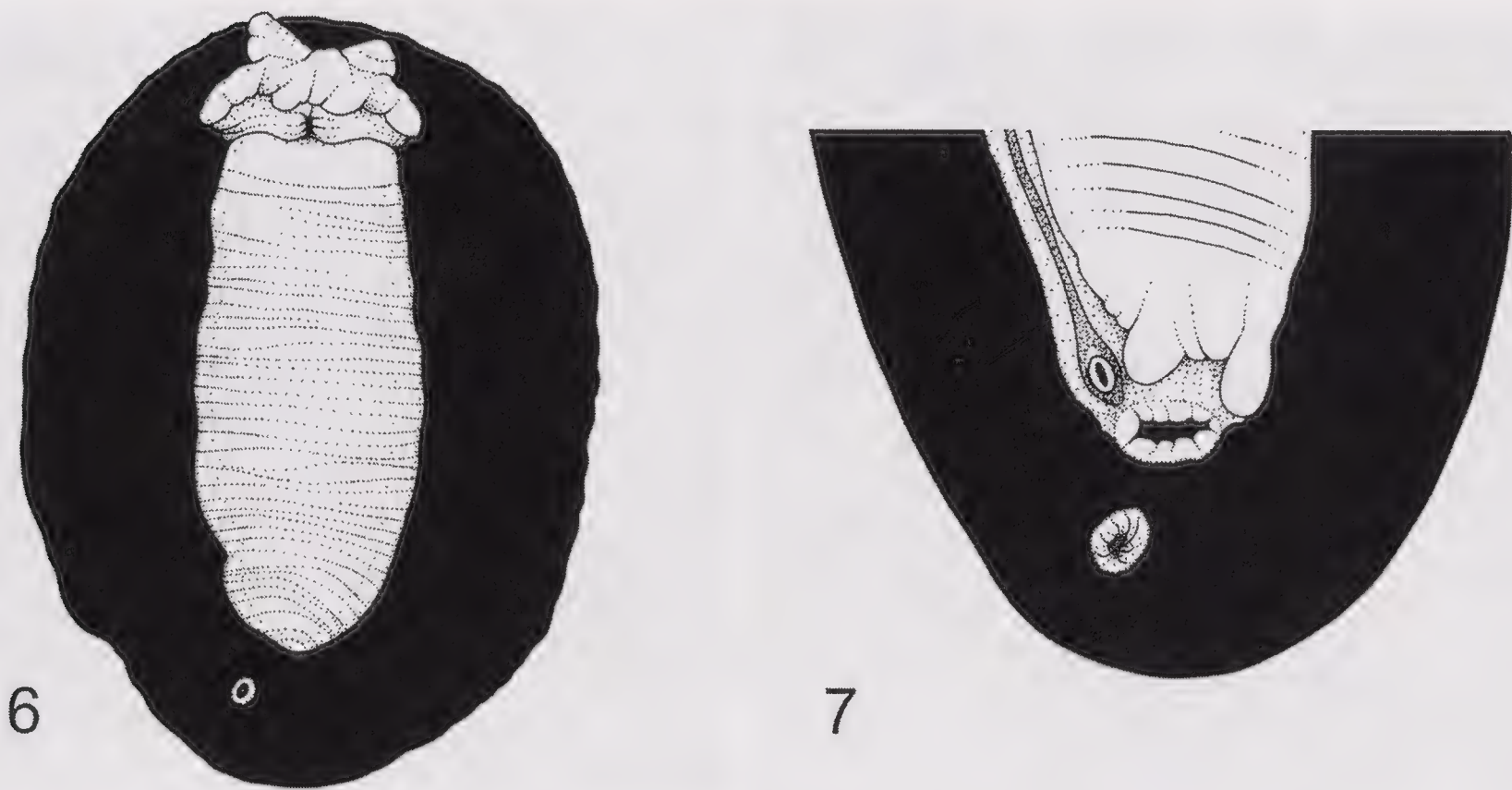
FIGS. 1–5. External morphology and color. FIG. 1: FLMNH 245191 #2, dorsal view, total length = 25 mm; FIG. 2: Same as Fig. 1, ventral view; FIG. 3: FLMNH 245191 #3, dorsal view, total length = 23 mm; FIG. 4: FLMNH 245777, left lateral view, total length of animal (from left to right) = 22 mm; FIG. 5: Same as Fig. 4, ventral view, total length = 22 mm (26 mm in width).

bluish black dorsal notum are found at higher elevation on both Panay (1,850 m, FLMNH 245142) and Mindoro (1,550 m, FLMNH 245788; 1,200 m, FLMNH 245776 & 245777). Populations with a brown dorsal notum are found at lower elevations, from 150 to 1,430 m in Panay, and from 400 to 600 m in Mindoro (type material of *apoikistes*). There is very little individual variation in dark bluish black populations, whereas there is high individual variation in lower-elevation populations: within each lot, the background color varies from light to dark brown mottled with darker areas of varying size and shapes. Finally, the individuals collected at 1,430 m in Panay are, on average, darker than from lower elevations: their color is intermediary between light brown (150–1,100 m) and dark bluish black (1,850 m). The pedal sole is whitish-beige in all specimens. The hyponotum varies from whitish-beige to dark brown; however, all specimens with a dark bluish black dorsal notum have a dark bluish black hyponotum, with or without a lighter margin.

External Morphology (Figs. 1–7)

The notum can be smooth or granular. Most individuals have both granular and smooth portions of notum, depending on how the notum retracted at fixation and preservation. The dorsal notum is oval and, usually longer than wide; some individuals are circular, and, occasionally, individuals may be wider than long. The hyponotum is horizontal. The body is gener-

ally flattened, although several individuals are almost conical (e.g., FLMNH 245777 #3, which measures 32/28 mm with a height of 22 mm). Dorsal gills are absent. Papillae with so-called “dorsal eyes” are present in all individuals; the number of papillae varies among individuals (larger individuals may have about 25 of them); all papillae bear one dorsal eye, except for one papilla, located in the center of the notum, which bears three dorsal eyes. The width of the hyponotum relative to the width pedal sole varies among individuals, even within the same lot: for example, within the lot FLMNH 245117, the ventral measurements are 1/16/1 mm (left hyponotum width / sole width / right hyponotum width) for spm #2 and 6/9/6 mm for spm #6. So, to use Labbé’s (1934) standard terms, the total width of the hyponotum (left and right sides added) can be superior ($H \gg S$) or inferior ($H \ll S$) to the width of the pedal sole. On the right side, a peripodial groove is present, from the anus to the buccal area. The anus is posterior, median, very close to the lateral side of the pedal sole. The position of the pneumostome on the hyponotum, relative to the notum margin and the lateral side of the pedal sole, varies from about 1/3 close to the pedal sole (i.e., 2/3 to the notum margin) to 1/2 close to the pedal sole (i.e., 1/2 to the notum margin). However, several individuals occasionally have a pneumostome that is 1/4 (e.g., FLMNH 245142) or 2/3 (e.g., FLMNH 245777) close to the pedal sole. The pneumostome is not median: it is close to the median line, but slightly on the right side. The position of



FIGS. 6, 7. External morphology. FIG. 6: FLMNH 245777 #1, ventral view, total length = 35 mm; FIG. 7: Same as Fig. 6, ventral view of the posterior end of the foot, with openings (anus, female aperture, and pneumostome), total width = 23 mm.

the female pore (posterior end of the peripodial groove, close to the anus) does not vary much among individuals. In the anterior region, the left and right ocular tentacles are superior to the mouth. In most preserved specimens, they are retracted inside the body. Eyes are located at the tip of the ocular tentacles. Inferior to the ocular tentacles, but superior to the mouth, the head bears a pair of oral lobes. The male aperture (opening of the penis and penial accessory gland) is located below and on the right lateral side of the right ocular tentacle.

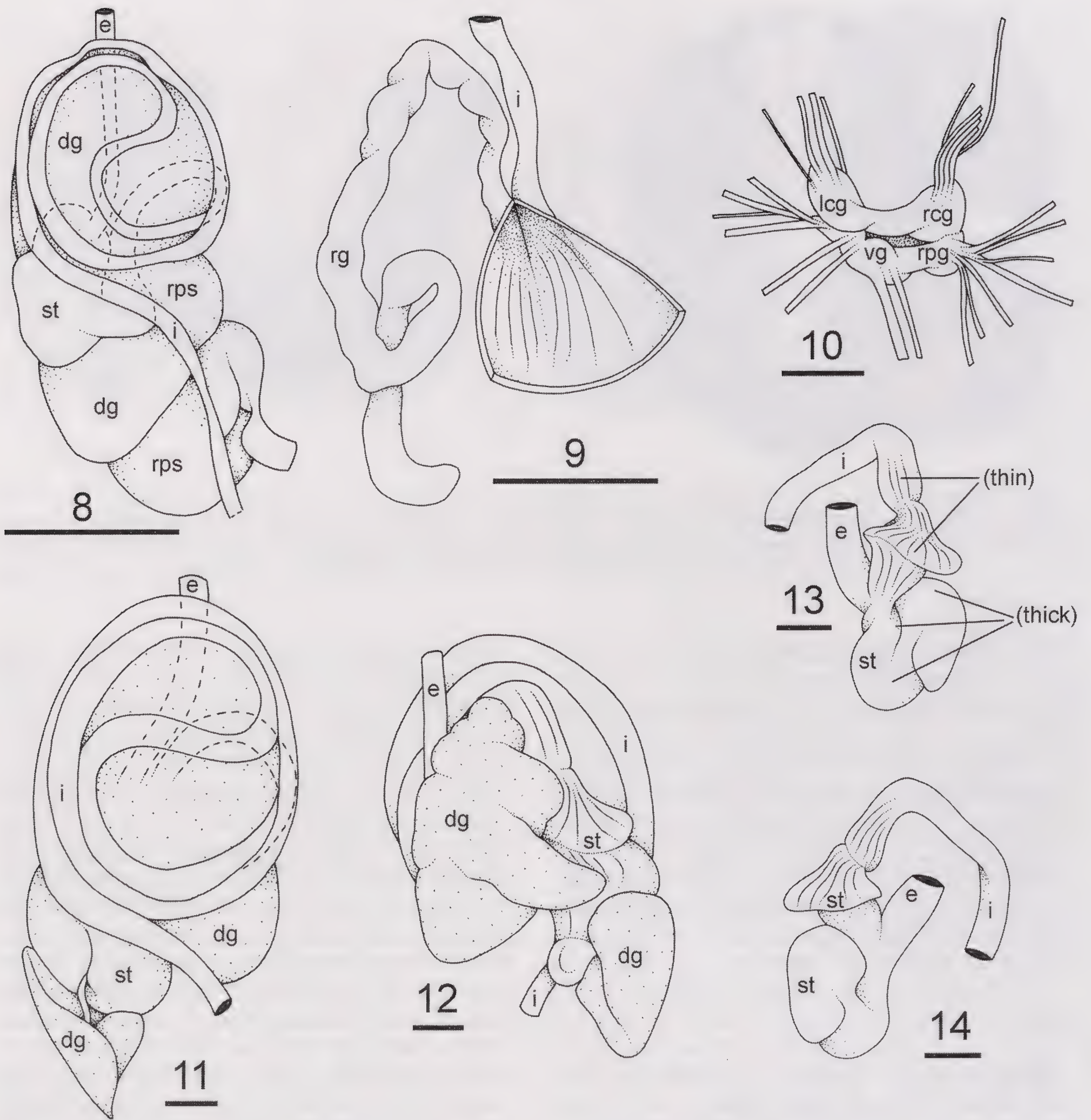
Visceral Cavity

Marginal glands (found in *Onchidella* species) are absent. The anterior pedal gland, lying free on the floor of the visceral cavity, below the buccal mass, is oval and flattened. The visceral cavity is not pigmented internally and not divided (the heart is not separated from the visceral organs by a membrane).

Digestive System (Figs. 8–26)

There are no jaws. The left and right salivary glands, heavily branched, join the buccal mass dorsally, on either side of the esophagus. The radula is in between two large postero-lateral muscular masses. Each radular row contains a rachidian tooth and two half rows of lateral teeth of similar size and shape. Radular formulae are: $65 \times (145-1-145)$ in FLMNH 245191 #1 (32 mm long), $55 \times (95-1-95)$ in

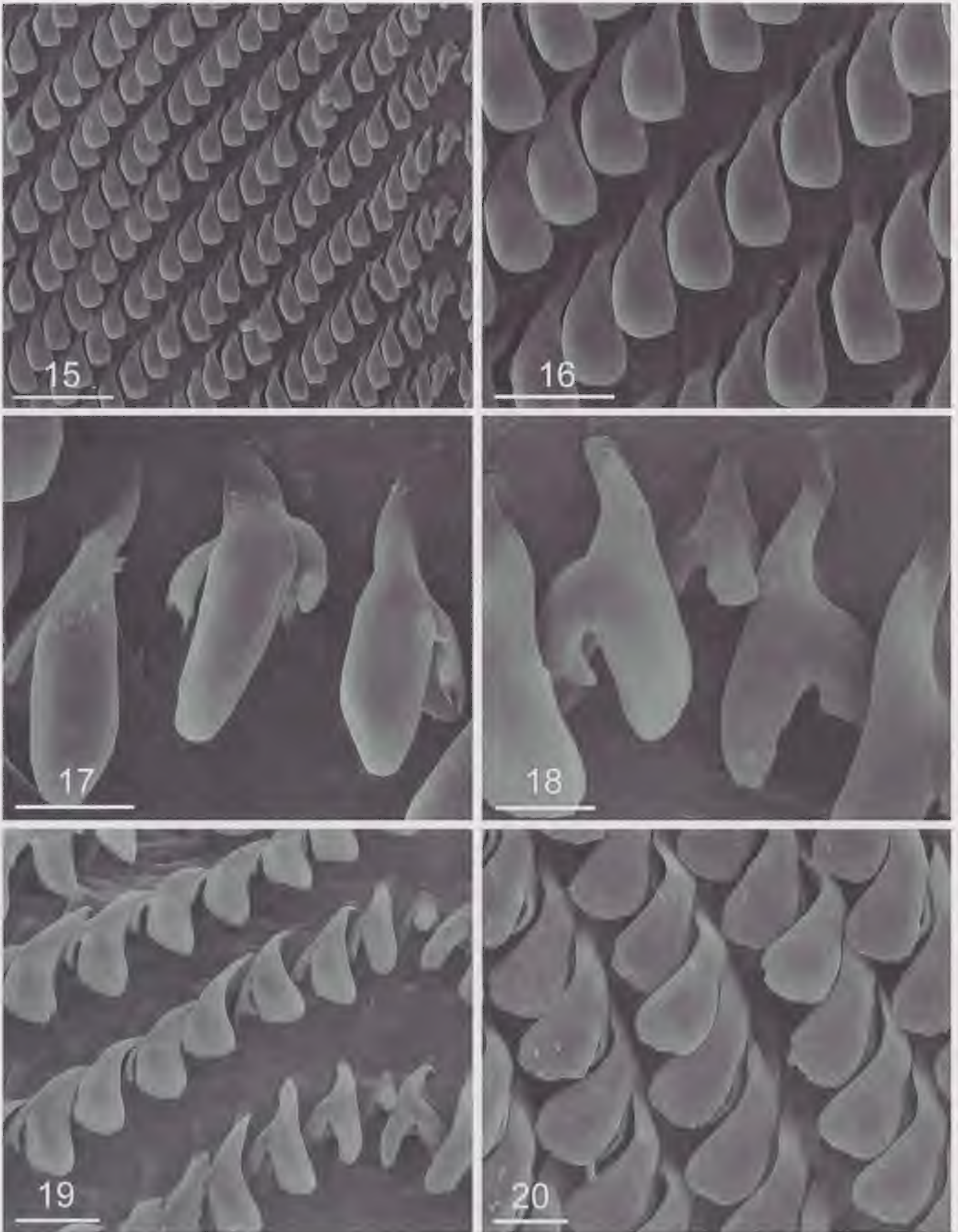
FLMNH 245549 #1 (25 mm), $75 \times (110-1-110)$ in FLMNH 245777 #1 (35 mm), $55 \times (80-1-80)$ in FLMNH 245117 #1 (20 mm), $85 \times (150-1-150)$ in FLMNH 245117 #2 (33 mm), $55 \times (80-1-80)$ in FLMNH 245117 #3 (19 mm), $60 \times (130-1-130)$ in FLMNH 245797 #2 (18 mm), $60 \times (125-1-125)$ in FLMNH 245776 #1 (26 mm), $70 \times (150-1-150)$ in paratype #1 of *apoikistes* (35 mm), and $70 \times (135-1-135)$ in paratype #2 of *apoikistes* (22 mm). The rachidian tooth is tricuspid: the median cusp is always present; the two lateral cusps, located on the two lateral branches of the base of the rachidian tooth, may be absent (especially in small rachidian teeth). Rachidian teeth tend to be smaller than lateral teeth (with a length of the rachidian tooth usually not exceeding $20 \mu\text{m}$), but exceptions are not uncommon (e.g., FLMNH 245777 #1); the size of the rachidian teeth varies within a single radula (older teeth are larger). The lateral surface of the base of the rachidian teeth is straight (neither concave nor convex). The half rows of lateral teeth form an angle of 45° with the rachidian axis. The lateral teeth seem to be simply unicuspid with a flattened and curved hook with a rounded to truncate tip (length usually $< 50 \mu\text{m}$), but there also is an outer, pointed spine on the lateral expansion of the base. In most cases, the lateral spine cannot be observed on a SEM picture because it is hidden below the hook of the next lateral tooth; however, when teeth are not too close (such as in the innermost and outermost regions), the lateral spines are conspicuously prominent.



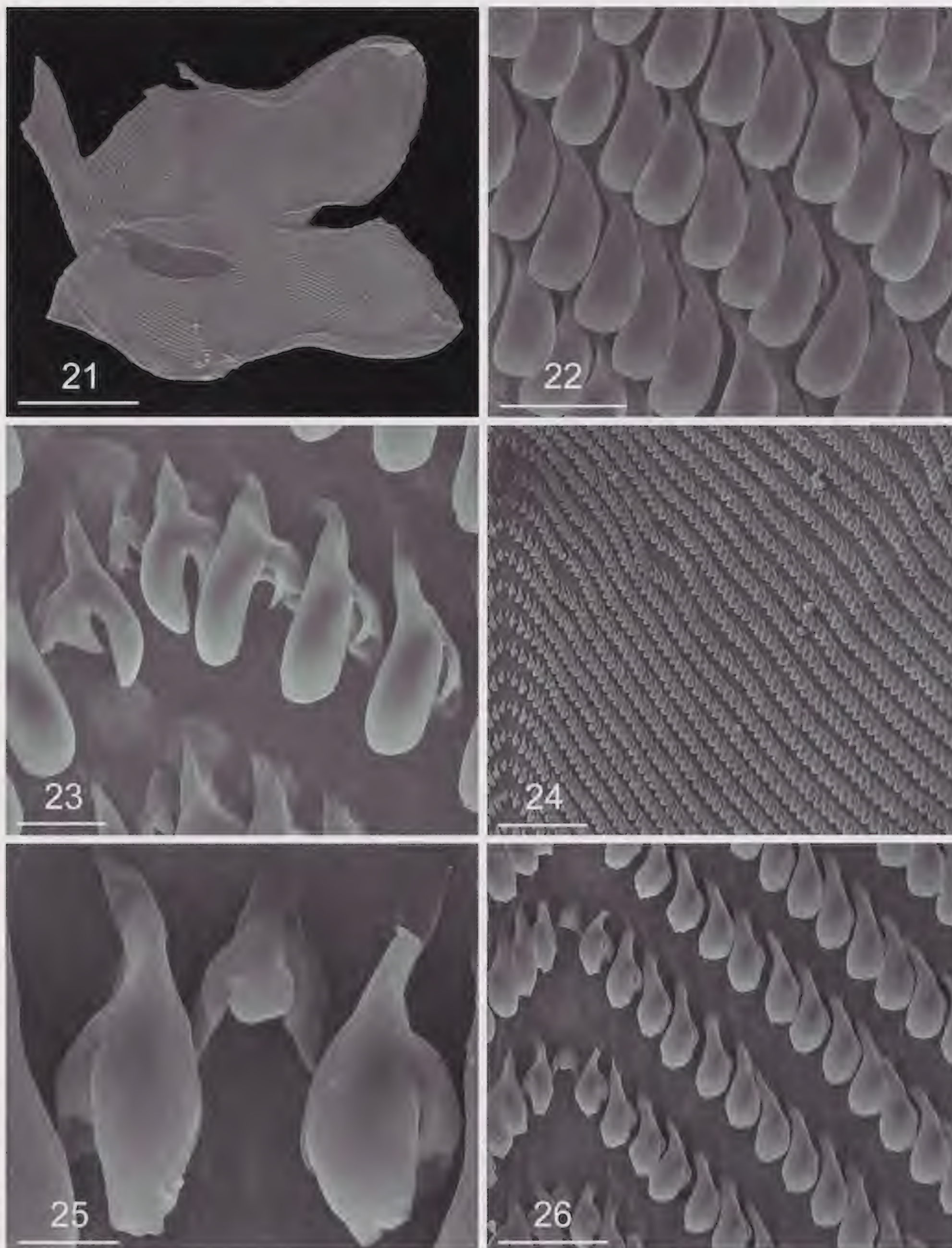
FIGS. 8–14. Digestive system and nervous system. FIG. 8: *P. apoikistes*, paratype #2, digestive system, dorsal view, scale = 5 mm; FIG. 9: *P. apoikistes*, paratype #2, rectal gland, scale = 3 mm; FIG. 10: *P. apoikistes*, paratype #2, central nervous system, dorsal view, scale = 1 mm; FIG. 11: FLMNH 245716 #4, digestive system, dorsal view, scale = 2 mm; FIG. 12: FLMNH 245716 #4, digestive system, ventral view, scale = 2 mm; FIG. 13: FLMNH 245716 #4, stomach, ventral view, scale = 2 mm; FIG. 14: FLMNH 245716 #4, stomach, dorsal view, scale = 2 mm.

With the exception of, sometimes, the first few innermost lateral teeth, the size and shape of the lateral teeth do not vary along the half row; nor do they vary among half rows; the shape of the tip of the hook varies among individuals, from clearly truncate to clearly rounded. The esophagus is narrow and straight; its internal folds cannot be seen externally. The esophagus

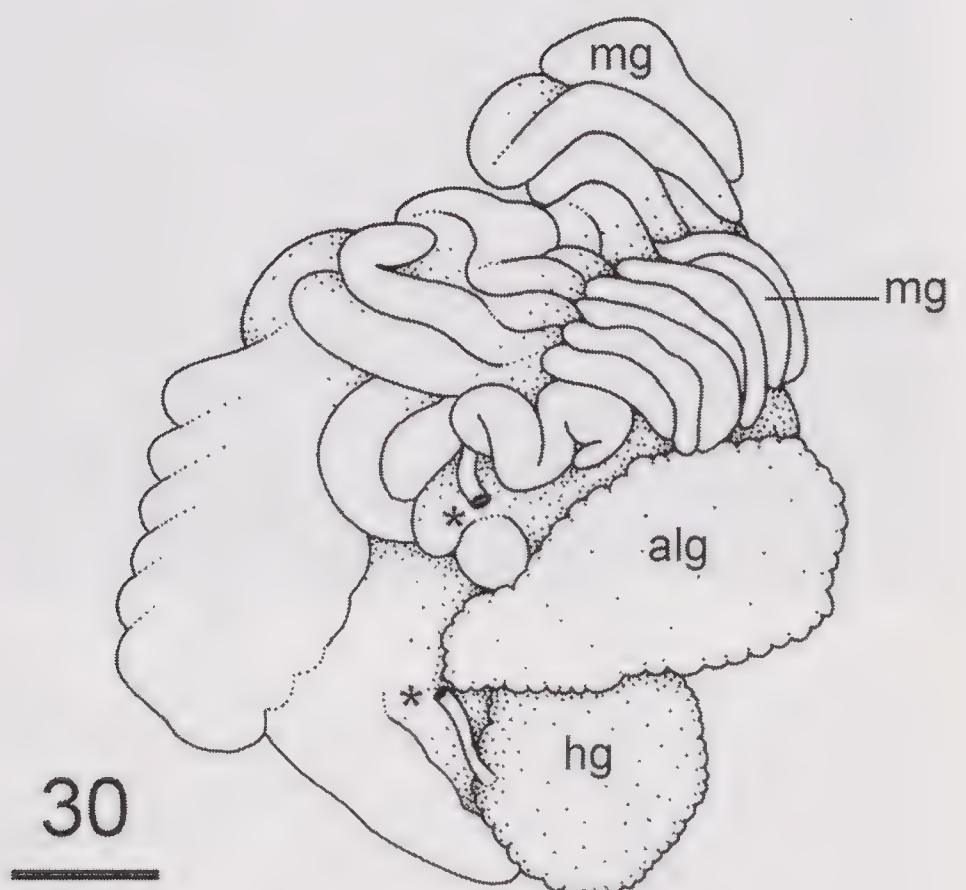
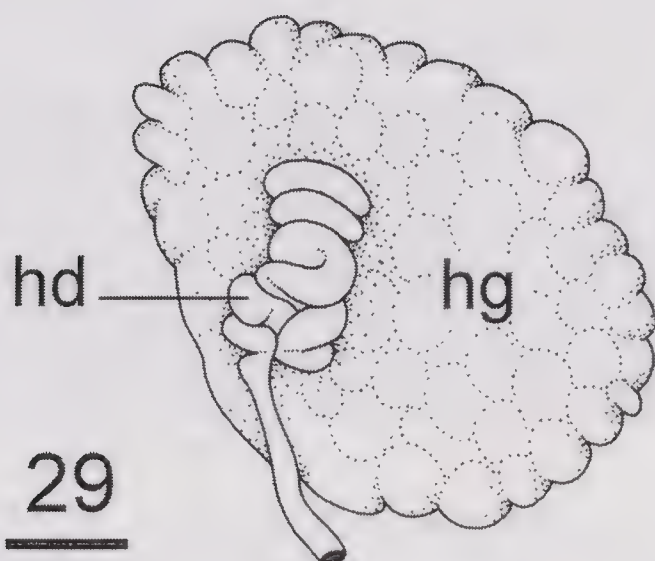
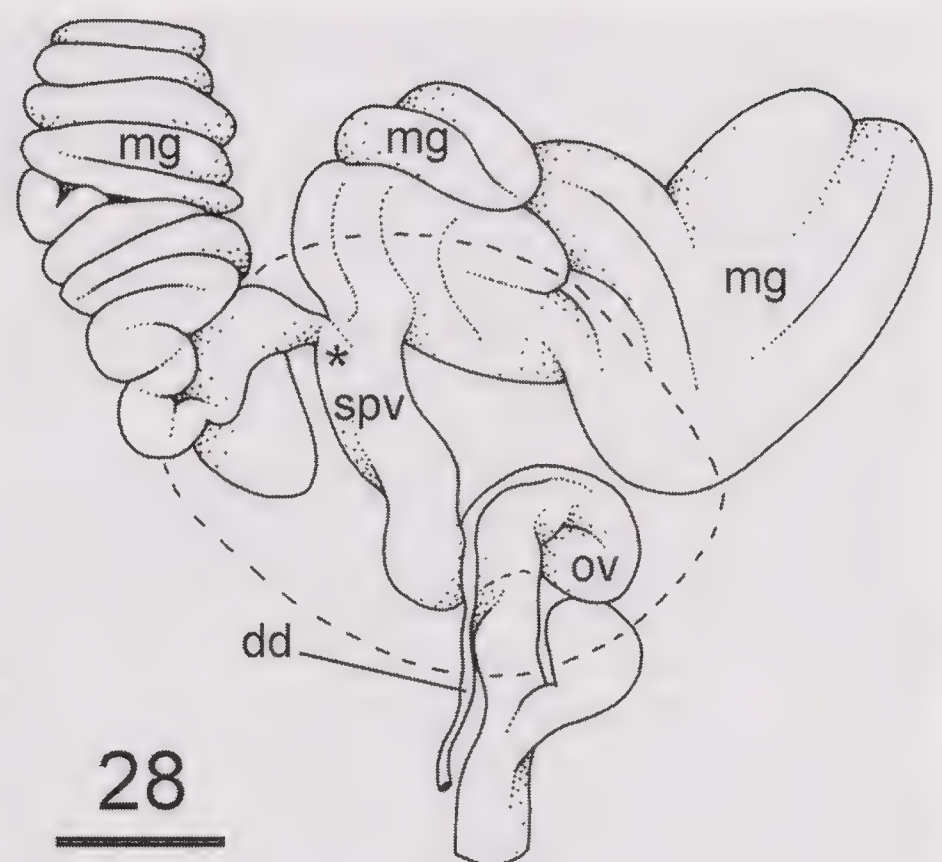
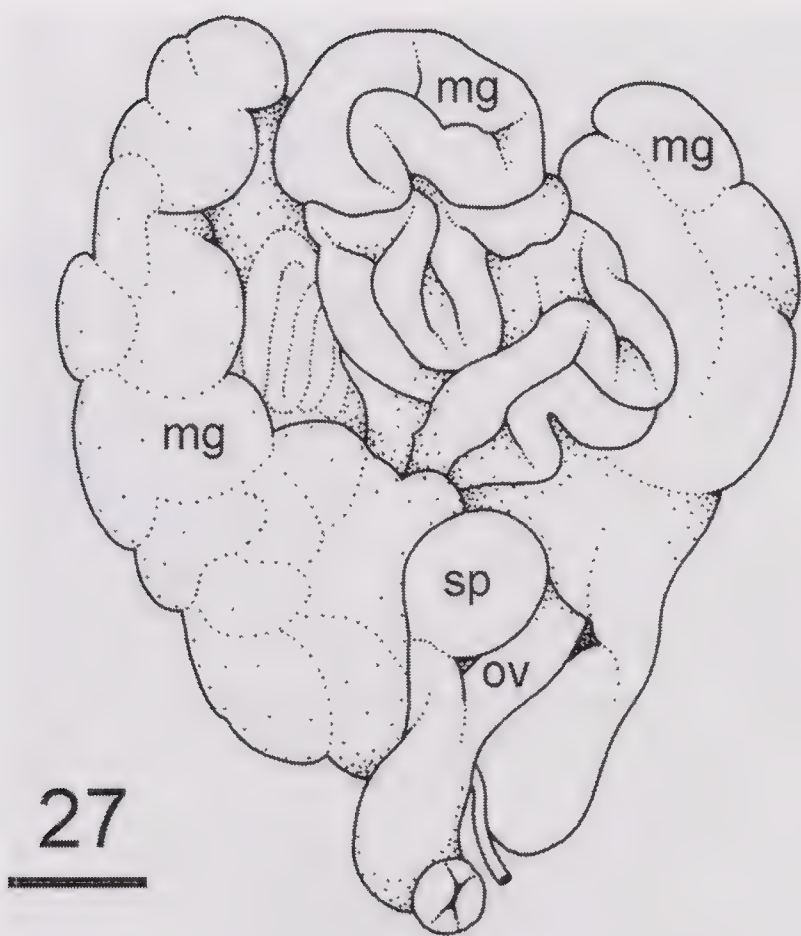
enters the stomach anteriorly. The stomach is located on the left dorsal side of the visceral mass and is mainly surrounded (except dorsally) by the digestive gland. It is a U-shaped sac divided internally in two compartments: the first compartment, which connects to the esophagus, is delimited by a thin layer of tissue, and the second compartment is delimited by a



FIGS. 15–20. Radula. FIG. 15: FLMNH 245777 #1, left, innermost teeth, scale = 100 μ m; FIG. 16: FLMNH 245777 #1, left, innermost teeth, scale = 50 μ m; FIG. 17: FLMNH 245777 #1, rachidian tooth, scale = 20 μ m; FIG. 18: FLMNH 245797 #1, rachidian tooth, scale = 10 μ m; FIG. 19: FLMNH 245797 #1, left, innermost teeth, scale = 20 μ m; FIG. 20: FLMNH 245797 #1, right, lateral teeth, scale = 20 μ m.



FIGS. 21–26. Radula. FIG. 21: *P. apoikistes*, paratype #1, radula, scale = 1 mm; FIG. 22: *P. apoikistes*, paratype #1, right, lateral teeth, scale = 50 μ m; FIG. 23: *P. apoikistes*, paratype #1, rachidian and innermost lateral teeth, scale = 20 μ m; FIG. 24: FLMNH 245117 #2, right lateral half rows (innermost part), scale = 200 μ m; FIG. 25: FLMNH 245117 #1, rachidian and two innermost lateral teeth, scale = 10 μ m; FIG. 26: FLMNH 245117 #1, rachidian and right innermost lateral teeth, scale = 50 μ m.

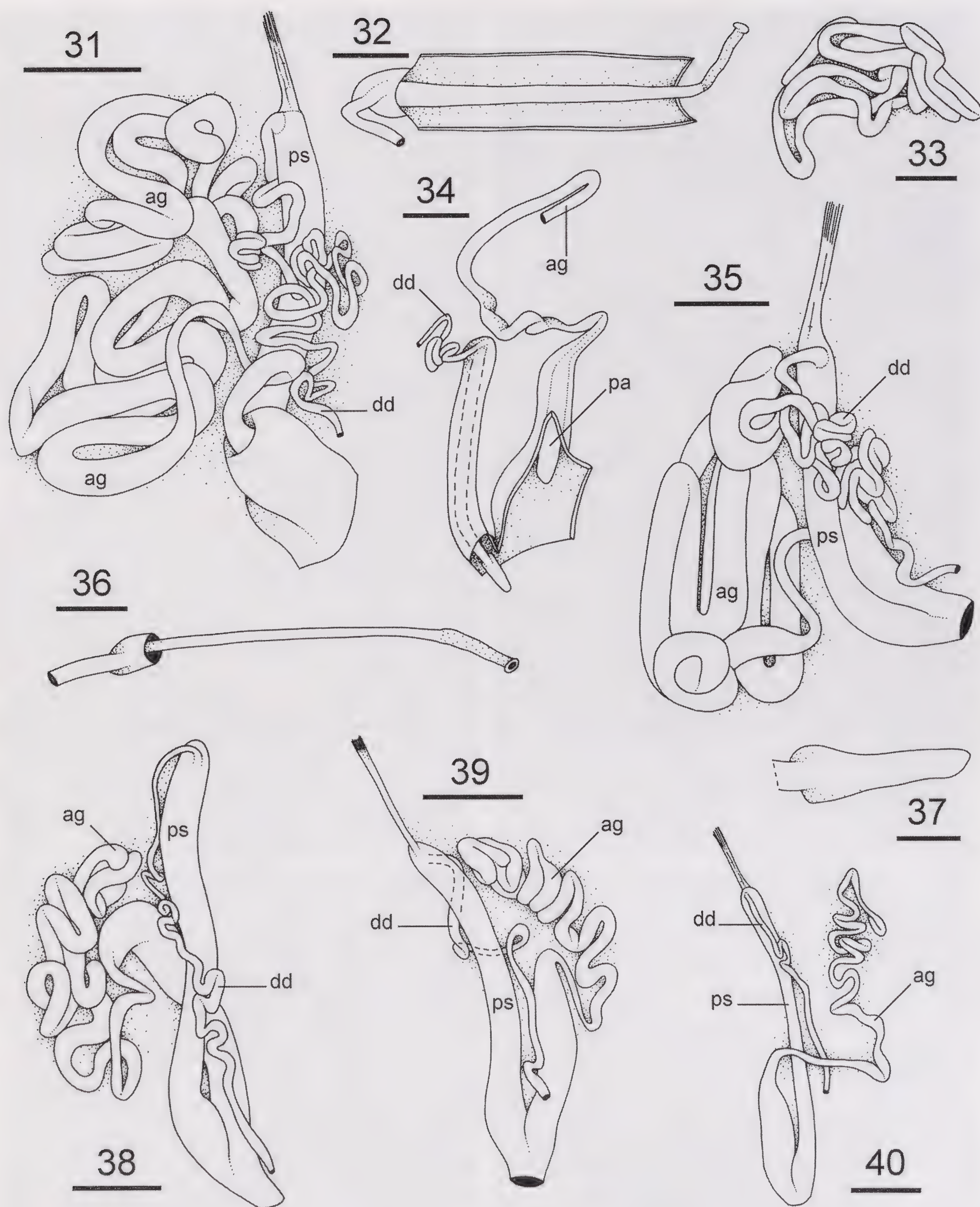


FIGS. 27–30. Reproductive system. FIG. 27: FLMNH 245716 #4, posterior part of the reproductive system, scale = 2 mm; FIG. 28: FLMNH 245716 #4, posterior part of the reproductive system (albumen gland within dotted line removed and different parts separated), asterisk indicates where hermaphroditic duct joins, scale = 3 mm; FIG. 29: FLMNH 245716 #4, hermaphroditic gland and duct, scale = 1 mm; FIG. 30: FLMNH 245716 #4, posterior part of the reproductive system, asterisks indicate where hermaphroditic duct was cut, scale = 2 mm.

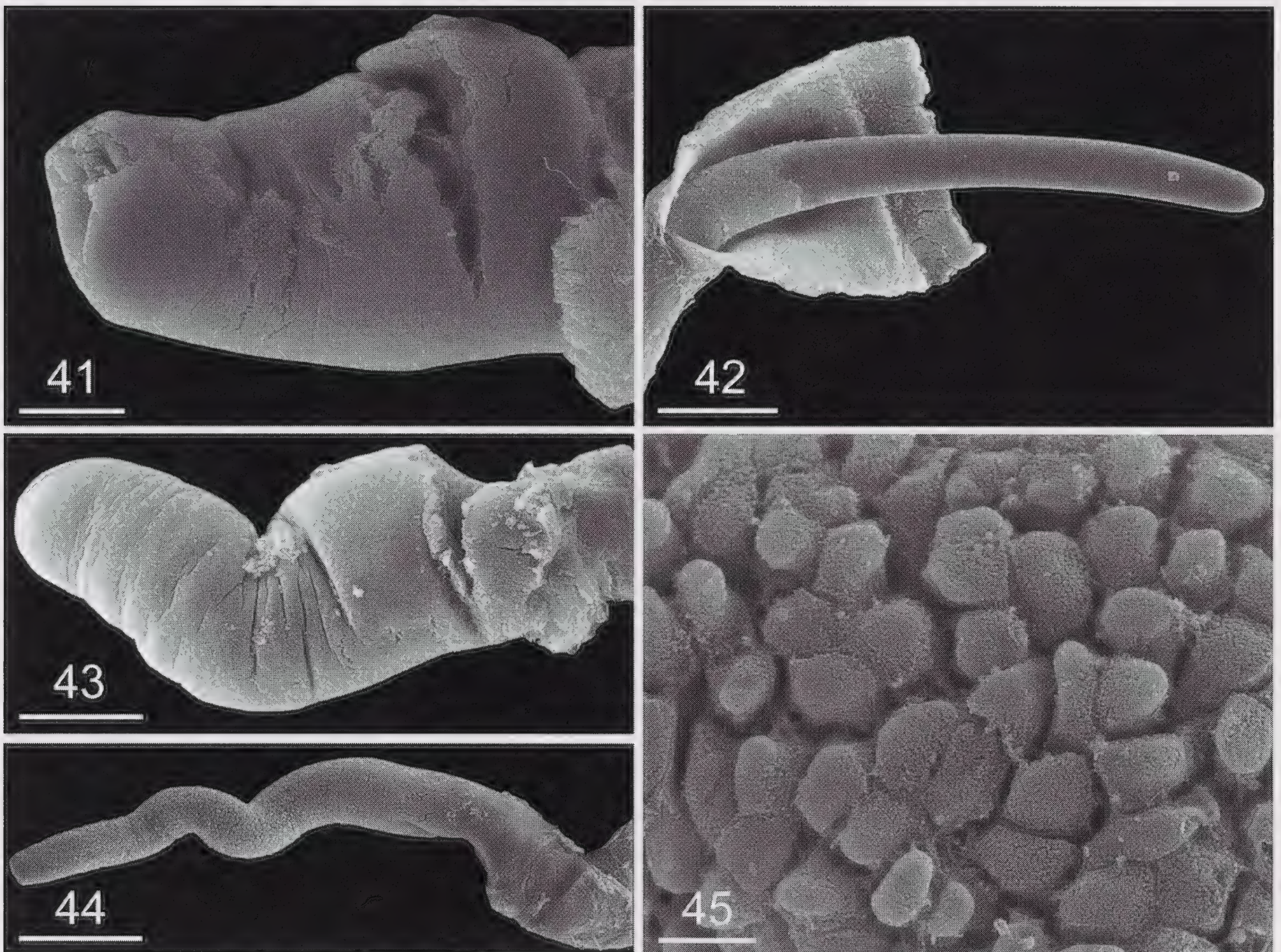
thick layer of tissue. The second compartment, externally, seems to be divided in more than one chamber, but only one chamber exists internally. No strong ridges were found on the internal surface of the stomach. The intestine is long, narrow, and of type II (characterized by two dorsal circles of the intestine), as defined by Labbé (1934). The narrow, convoluted tube of the rectal gland (unknown function) covers the postero-dorsal visceral mass and opens in the pulmonary complex, near the anus; its proximal end lies freely in the visceral cavity.

Nervous System (Fig. 10)

The circum-esophageal nerve ring is post-pharyngeal and pre-esophageal. The two cerebral ganglia are conspicuously not fused, separated by a thick cerebral commissure that is as large as each cerebral ganglion. Pleural and pedal ganglia are also distinct. The visceral commissure is very short and mainly consists of the visceral ganglion, which is on the left side of the visceral loop. Cerebro-pleural and pleuro-pedal connectives are short. In fact, pleural



FIGS. 31–40. Reproductive system. FIG. 31: *P. apoikistes*, paratype #1, male anterior parts, scale = 2 mm; FIG. 32: *P. apoikistes*, paratype #2, penis (penial sheath opened), scale = 1 mm; FIG. 33: *O. montana*, paratype #2, flagellum of male accessory gland (not represented in Tillier, 1983: Fig. 3), scale = 1 mm; FIG. 34: *O. montana*, paratype #2, male anterior parts (flagellum of accessory gland cut), scale = 1 mm; FIG. 35: FLMNH 245777 #1, male anterior parts, scale = 2 mm; FIG. 36: FLMNH 245777 #1, penis (penial sheath removed), scale = 1 mm; FIG. 37: FLMNH 245777 #1, distal papilla of male accessory gland, scale = 250 μ m; FIG. 38: FLMNH 245117 #3, male anterior parts, scale = 1 mm; FIG. 39: FLMNH 245117 #1, male anterior parts, scale = 1 mm; FIG. 40: FLMNH 245797 #1, male anterior parts, scale = 1 mm.



FIGS. 41–45. Male accessory gland. FIG. 41: FLMNH 245117 #1, distal papilla (immature) of accessory gland, scale = 50 μ m; FIG. 42: FLMNH 245117 #2, fully developed, hollow spine of accessory gland, scale = 200 μ m; FIG. 43: FLMNH 245117 #3, distal papilla (immature) of accessory gland, scale = 100 μ m; FIG. 44: FLMNH 245117 #4, distal papilla (intermediate stage) of accessory gland, scale = 250 μ m; FIG. 45: FLMNH 245117 #4, same as before, surface covered with soft tissue, scale = 10 μ m.

and cerebral ganglia are touching each others. Nerves from the cerebral ganglia innervate the buccal area and the ocular tentacles, and, on the right side, the male anterior organs (penial accessory gland and penial complex). Nerves from the pedal ganglia innervate the foot. Nerves from the pleural ganglia innervate the lateral and dorsal regions of the mantle. Nerves from the visceral ganglia innervate the visceral organs.

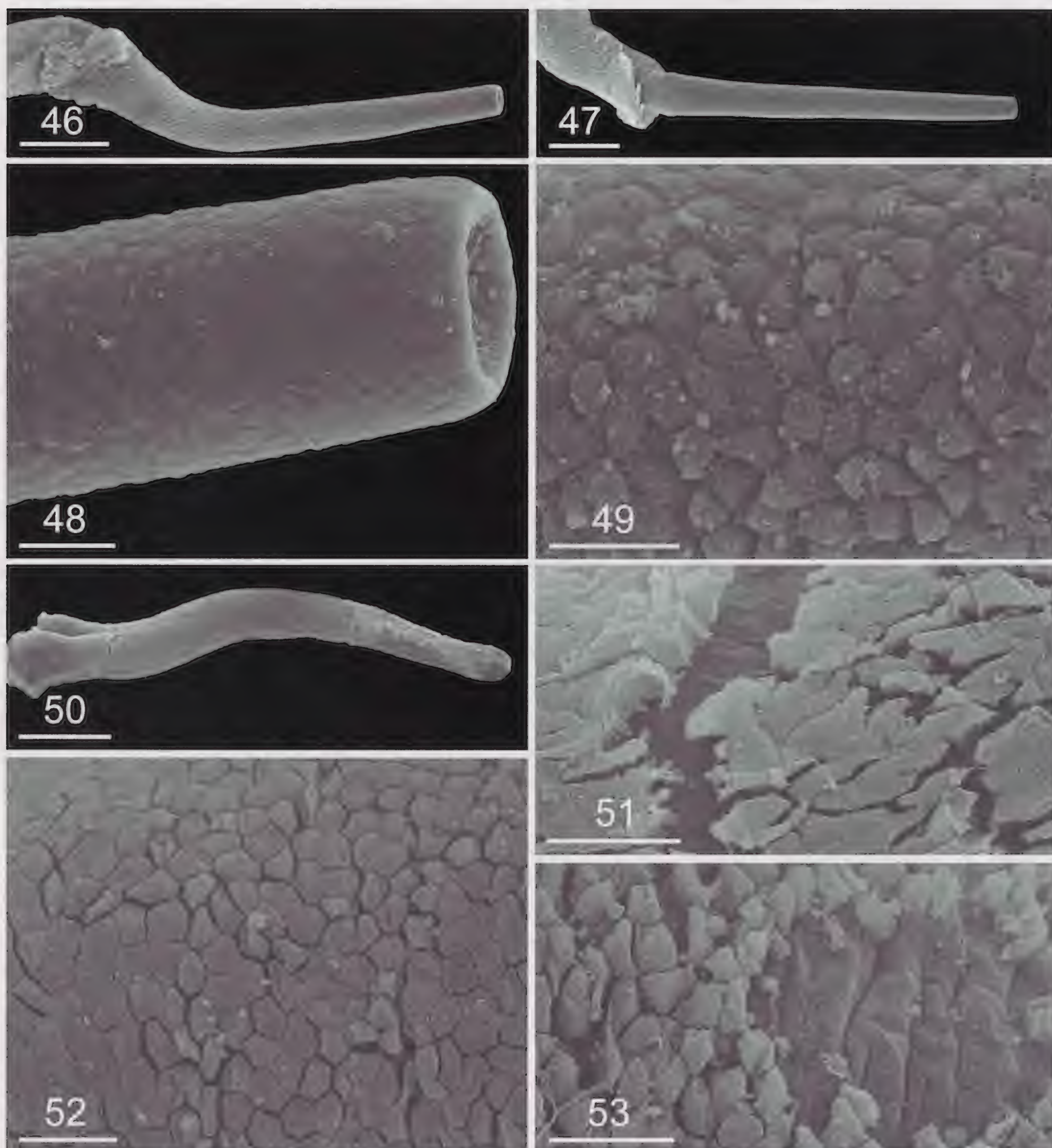
Pallial Complex

The heart is enclosed in the pericardium, located on the right side of the middle of the body cavity. The ventricle, anterior, gives an anterior vessel supporting several anterior organs, such as the buccal mass, the nervous system, and the copulatory complex. The auricle is posterior. The kidney is distinctly asymmetrical, the right part being much more developed (it runs up

to the heart level) than the left part (remains posterior). The kidney is intricately attached to the respiratory complex, a lung in two left and right, asymmetrical parts.

Reproductive System (Figs. 27–40)

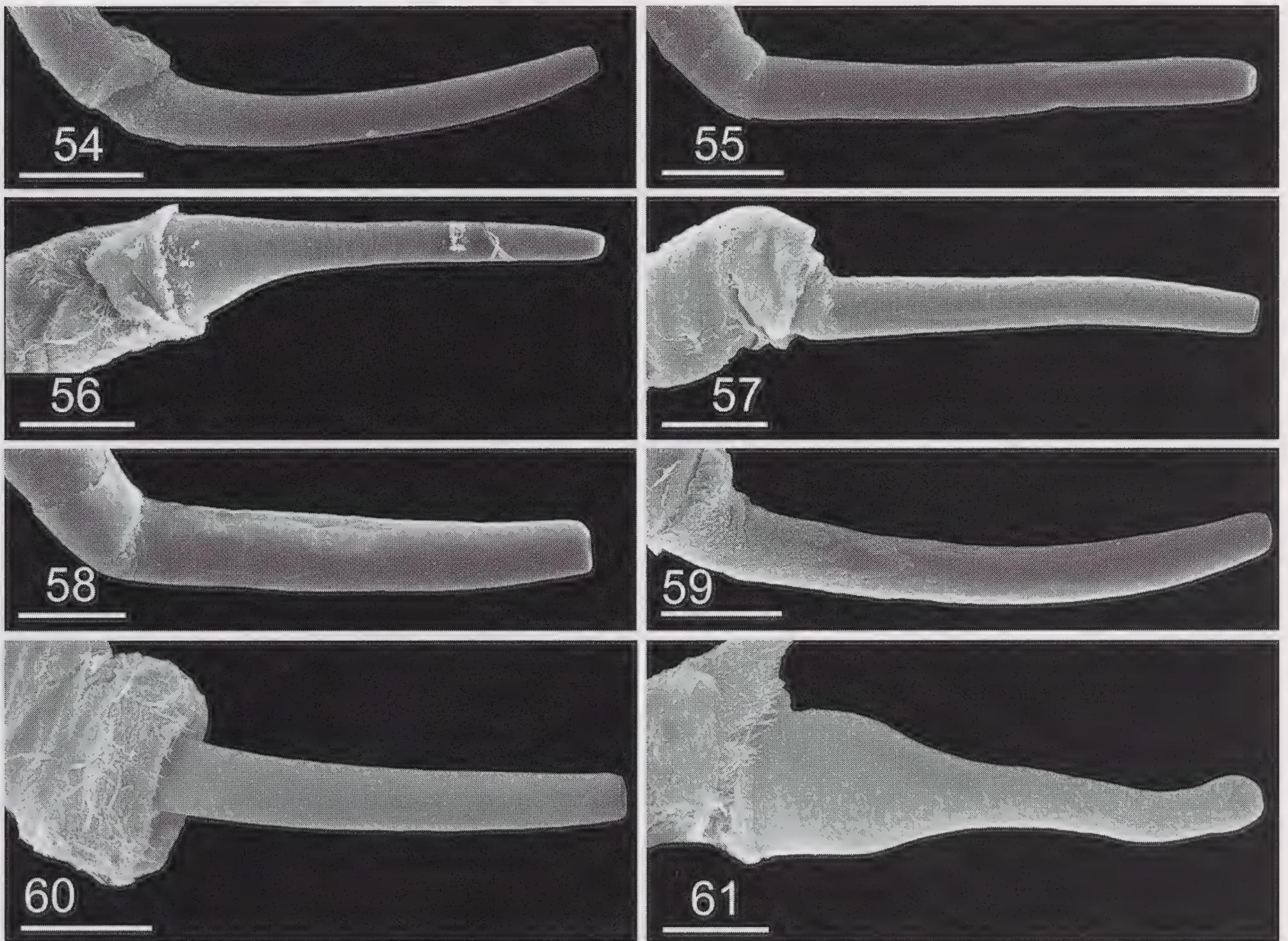
Mature individuals have large, fully developed, female organs (e.g., large albumen and mucus glands), whereas immature individuals may have small, inconspicuous, or simply no female organs, while their anterior male parts are not fully developed either. Sexual maturity is correlated with size: all (dissected) specimens longer than 23 mm (preserved) were sexually mature; 23 mm-long specimens may be mature (*apoikistes* paratype #2; FLMNH 245776 #2) or not (FLMNH 245117 #5); all specimens < 23 mm were immature, with the exception a few specimens from Panay Island (FLMNH 245797



FIGS. 46–53. Male accessory gland. FIG. 46: FLMNH 245191 #1, fully developed, hollow spine of accessory gland, scale = 250 μ m; FIG. 47: FLMNH 245191 #2, fully developed, hollow spine of accessory gland (but surface still covered with soft tissue), scale = 200 μ m; FIG. 48: FLMNH 245191 #2, hollow spine tip, scale = 25 μ m; FIG. 49: FLMNH 245191 #2, hollow spine still covered with soft tissue, scale = 25 μ m; FIG. 50: FLMNH 245191 #3, fully developed, hollow spine of accessory gland (surface still covered with soft tissue), scale = 250 μ m; FIG. 51: FLMNH 245191 #3, surface of spine still covered with soft tissue, scale = 20 μ m; FIG. 52: FLMNH 245191 #3, surface of spine still covered with soft tissue, scale = 20 μ m; FIG. 53: FLMNH 245191 #3, surface of spine still covered with soft tissue, scale = 20 μ m.

#2, #4, and #5, 18 mm, 16 mm, and 17 mm long, respectively), but those specimens are more conical than flattened, and were alive probably much longer. The hermaphroditic

gland is a single mass, joining to the spermoviduct through the hermaphroditic duct (conveys eggs and the autosperm). There is no vesicula seminalis (caecum) along the hermaphroditic



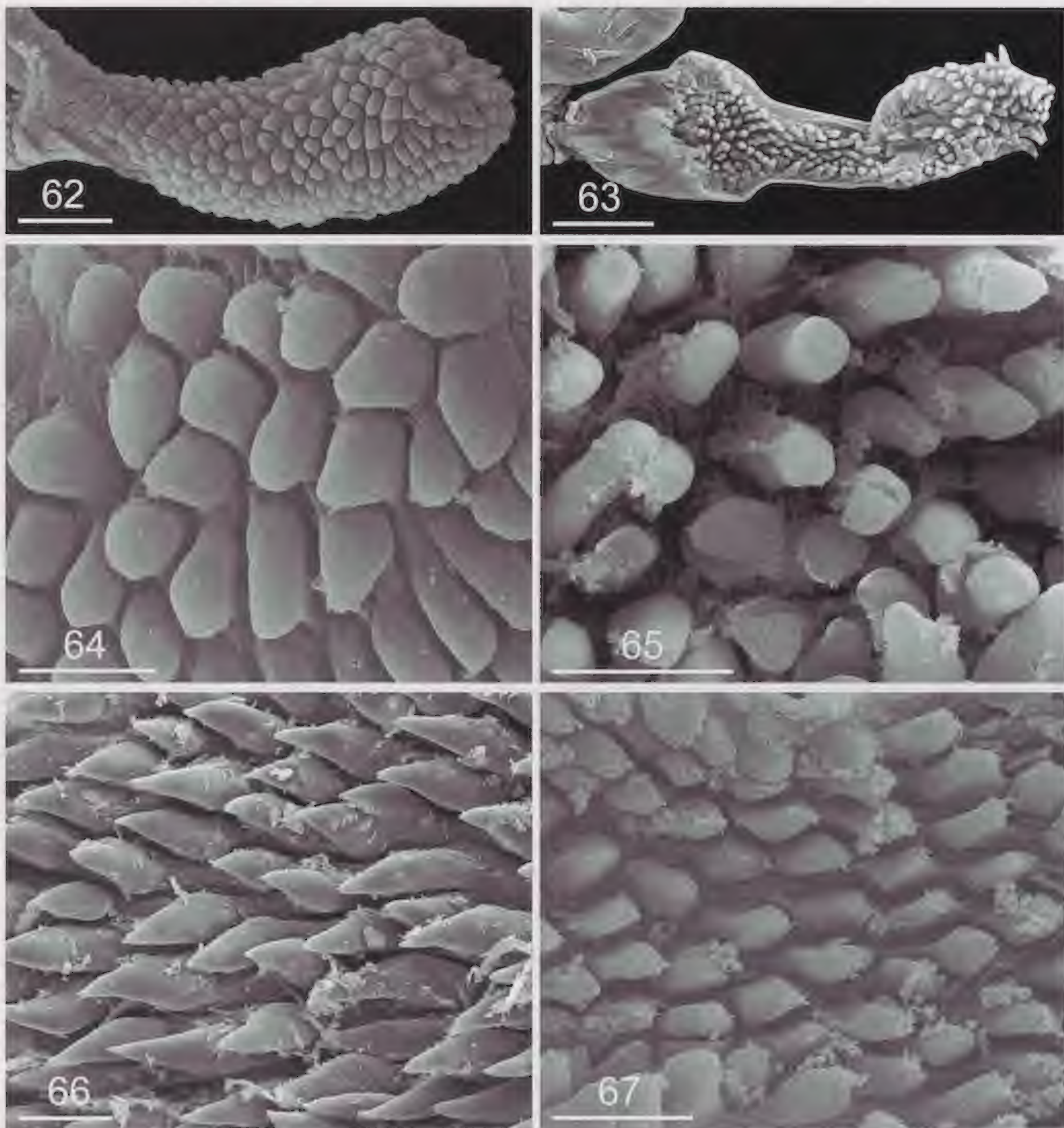
FIGS. 54–61. Male accessory gland. FIG. 54: *P. apoikistes*, paratype #1, fully developed, hollow spine of accessory gland, scale = 250 μ m; FIG. 55: *P. apoikistes*, paratype #2, fully developed, hollow spine of accessory gland, scale = 200 μ m; FIG. 56: FLMNH 245549 #1, fully developed, hollow spine of accessory gland, scale = 200 μ m; FIG. 57: FLMNH 245776 #1, fully developed, hollow spine of accessory gland, scale = 200 μ m; FIG. 58: FLMNH 245777 #1, fully developed, hollow spine of accessory gland, scale = 150 μ m; FIG. 59: FLMNH 245777 #2, fully developed, hollow spine of accessory gland, scale = 200 μ m; FIG. 60: FLMNH 245797 #2, fully developed, hollow spine of accessory gland, scale = 200 μ m; FIG. 61: FLMNH 245797 #3, distal papilla (immature) of accessory gland, scale = 150 μ m.

duct. Two highly convoluted mucous glands open where the hermaphroditic duct becomes the spermovi duct (conveys eggs, exosperm, and autosperm). For its first proximal half, the spermovi duct is not divided, at least externally. The prostate, not distinct externally, may be located within the walls of the spermovi duct. The spermovi duct is completely embedded within the albumen gland (which also covers part of the mucous glands). The opening of the albumen gland into the spermovi duct is unclear, but is likely distal to the opening of the mucous gland. Distally, the male duct becomes the vas deferens (conveys the autosperm up to the cephalic region) and is separate from the oviduct. The free oviduct (conveys the eggs up to the female opening and the exosperm from the female opening up to the fertilization chamber,

near the proximal end of the spermovi duct) is about as long as the spermovi duct itself. Distally, the oviduct becomes the vagina, which is shorter than the free oviduct (about half its size). The ovate-spherical spermatheca (storage of exosperm) connects to the distal region of the oviduct through a short, wide duct.

Male (Anterior) Parts (Figs. 41–75)

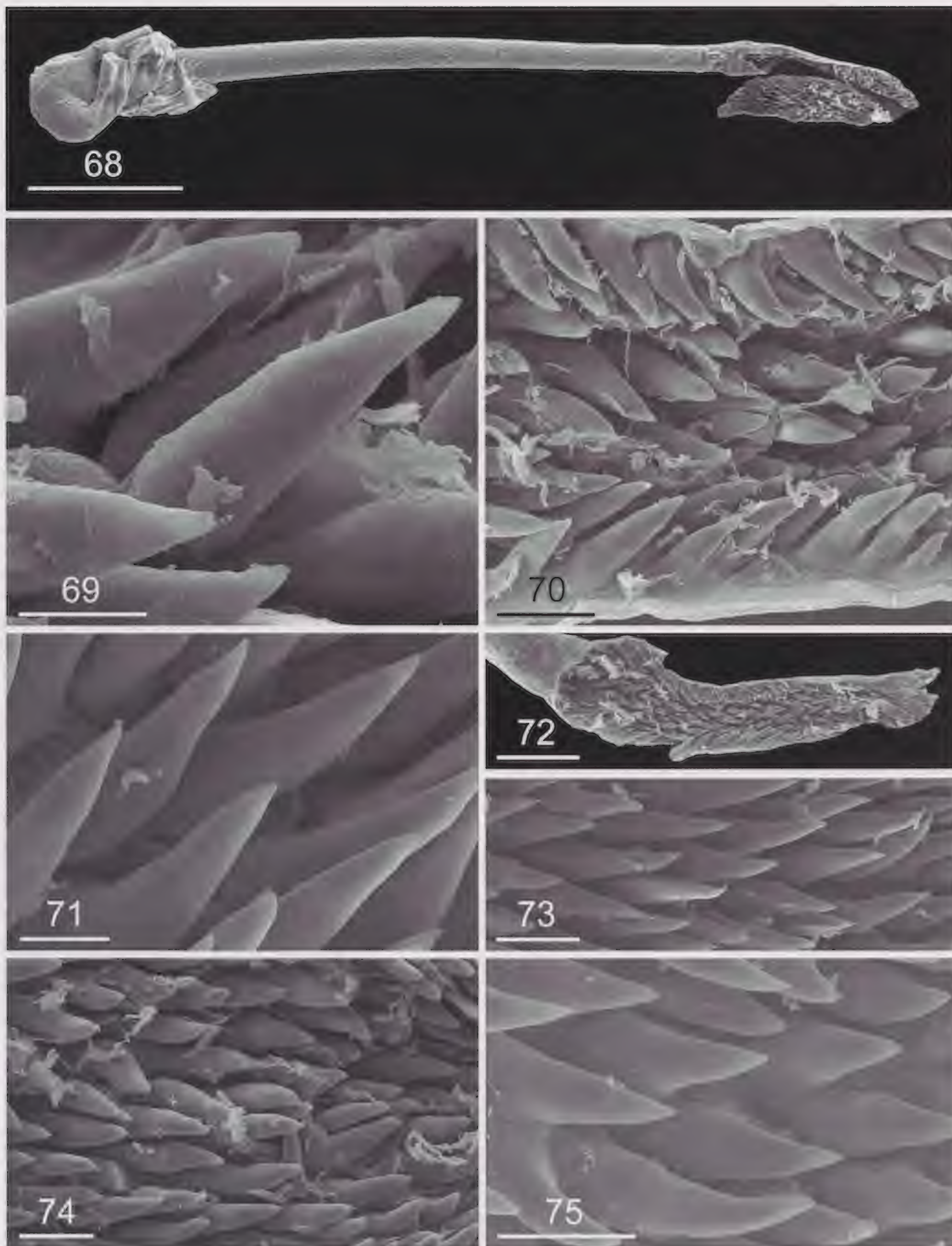
The male anterior organs consist of the penial complex (penis, penial sheath, deferent duct, retractor muscle) and the accessory penial gland (flagellum, papilla or spine). The penis and the penial gland share the same vestibule and the same male aperture. The internal surface of the vestibule is smooth (not covered by strong ridges or hooks).



FIGS. 62–67. Penis. FIG. 62: FLMNH 245117 #1, immature, evaginated distal end of penis (hooks not fully formed), scale = 150 μ m; FIG. 63: FLMNH 245117 #5, immature distal end of penis (hooks not fully formed), scale = 250 μ m; FIG. 64: FLMNH 245117 #1, same as Fig. 58, details, scale = 50 μ m; FIG. 65: FLMNH 245117 #5, same as Fig. 59, details, scale = 50 μ m; FIG. 66: FLMNH 245117 #2, hooks (fully formed) of distal end of penis, scale = 50 μ m; FIG. 67: FLMNH 245797 #1, hooks (not fully formed) of distal end of penis, scale = 50 μ m.

The length of the flagellum of the penial gland varies among individuals, depending on whether animals are mature or not. In mature individuals, the flagellum of the penial gland, long and heavily coiled, covers the dorsal surface of the buccal mass and is the first organ one sees in the anterior region when dissecting an animal in dorsal view. In individuals that are not

mature, the flagellum is much shorter; although it is coiled, it does not cover the dorsal surface of the buccal mass. Distally, the flagellum ends into a soft papilla (in immature individuals) or a hard, hollow spine (in mature individuals). The papilla and the spine are located at exactly the same position (distal end of the penial gland) and are thus homologous structures. Both



FIGS. 68–75. Penis. FIG. 68: FLMNH 245549 #1, penis (proximal stalk and distal hooks), scale = 1 mm; FIG. 69: FLMNH 245549 #1, penial hooks, scale = 20 μ m; FIG. 70: FLMNH 245776 #1, penial hooks, scale = 50 μ m; FIG. 71: *P. apoikistes*, paratype #2, penial hooks, scale = 20 μ m; FIG. 72: FLMNH 245776 #1, penial hooks, scale = 250 μ m; FIG. 73: *P. apoikistes*, paratype #2, penial hooks, scale = 50 μ m; FIG. 74: FLMNH 245777 #1, penial hooks, scale = 50 μ m; FIG. 75: FLMNH 245191 #1, penial hooks, scale = 50 μ m.

structures are hollow, likely to convey to the outside whatever is produced within the cells of the flagellum. During the development of male parts, the distal end of the flagellum first differentiates into a papilla, which is actually a duct (with a hole at its tip). This condition is found in all immature specimens. In most stations (e.g., FLMNH 245117), the immature specimens are shorter than 20 mm; exceptionally (FLMNH 245797), the immature specimens are shorter than 16 mm. The shape of the papilla changes ontogenetically, which is illustrated in all stations in which several immature specimens were available: at its earliest stage, it is simply conical (FLMNH 245117 #1) and measures only about 250 μm in length; then, it lengthens, becomes narrower (FLMNH 245117 #3), and reaches a maximum length of 1 mm; soft papillae are not straight for most of their development (FLMNH 245117 #4) and only become straight when in the process of becoming a hollow spine (FLMNH 245191 #3). The hollow spine of the penial gland is produced inside the papilla, which disappears when the hollow spine is fully formed; the external surface of early papillae is smooth, whereas the surface of late papillae forms cuboidal, separate masses of tissues ready to fall off (FLMNH 245117 #4) after the hollow spine is being formed (FLMNH 245191 #3, illustrates a superficial layer of tissue falling off from the smooth surface of the hollow spine); traces of superficial masses of tissue are sometimes observed on the surface of the (freshly formed) spines (FLMNH 245117 #2); fully mature spines, however, are completely smooth and bear no trace of any tissue from the papilla. Fully developed hollow spines measure from 0.7 to 1 mm in length, and about 100 μm in diameter. Their base is slightly larger and measures up to 200 μm in diameter. Also, spines are slightly bent at the base, although the angle varies among individuals but does not exceed 30° (and the way the spine is deposited on the stub may also influence our view). Both the papilla and the hollow spine are protected by a sheath that opens into the common male vestibule (in which the penial sheath opens too).

The penial sheath protects the penis located at the distal end of the deferent duct. The retractor muscle marks the separation between the penial sheath and the deferent duct. The latter is highly convoluted and coiled (many loops) in mature specimens; in immature specimens, it is much less coiled, and sometimes even only slightly coiled (FLMNH 245117 #1). The deferent duct is much narrower than the flagel-

lum (~ 50 vs. $250 \mu\text{m}$). Penial morphology is affected by age and sexual maturity. The penis of mature specimens consists of a proximal long, narrow, straight, and quite rigid stalk of 4 to 5 mm, followed by a distal soft tube densely covered internally by hooks of about 1 mm in length. Hooks are conical: they measure about the same length (about 80 μm) for a diameter of about 20 μm at their base. Hooks form a dense internal cover, with about 100 hooks on a surface of about 200 μm by 200 μm . Early in the penial development, soft papillae are observed instead of hooks (FLMNH 245117 #1 & 5, FLMNH 245797 #1); hooks are formed inside papillae (one hook per papilla).

DISCUSSION

Intra-Specific Variation

Color variation (of preserved specimens) is correlated with elevation gradient. Unfortunately, this correlation cannot be discussed in greater detail because the natural habitats of the populations studied here are unknown. In any case, populations with a light brown notum (preserved) live at lower elevations both in Panay (150–1,100 m) and Mindoro (400–600 m). Individuals with a dark bluish-black notum live at higher elevation in Panay (1,850 m) and Mindoro (1,200–1,550 m). The dorsal color of preserved individuals collected at 1,430 m from Panay is intermediary between light brown (150–1,100 m) and dark bluish black (1,850 m). Light brown individuals do not have a homogeneous brown back: their notum is always mottled with darker areas. All those specimens are identical anatomically, and there is no reason to distinguish two species based on dorsal color (one species with a bluish-black notum, and another with a brown dorsal notum). This result seems to confirm one of Britton's (1984: 181) statements on the use of color in onchidiids: "Unlike the situation in opisthobranchs, color is of very limited use in identifying onchidiaceans." More broadly, several studies have shown that the use of color pattern for taxonomic purposes in terrestrial slugs is problematic due to high intra-specific variation (e.g., Backeljau et al., 1996; Jordaens et al., 2006). Finally, it is important to keep in mind that the color variation discussed here is exclusively based on preserved specimens, and that the color of live animals might differ.

Several external characters merit to be commented on, as they were used for high-level

classification or as species distinctive features. Labbé (1934) used the presence / absence of gills on the dorsal notum as a primary feature to separate onchidiids in Dendrobranchiatae vs. Abranchiatae. This division is likely invalid, as argued by Britton (1984). Whether the notum is smooth or granular varies a great deal, depending on preservation, and should probably not be used for distinguishing species. Another feature that has been commonly used in onchidiid taxonomy is the size of the hyponotum (H: width of left and right sides) relative to the width of the pedal sole (S). For instance, Labbé (1934) asserted that $H < S$ in *Onchidium* and *Paraoncidium*, whereas $H > S$ or $= S$ in *Platevindex* (*Oncis*) and *Semperoncis* (*Semperella*). This character, however, varies among individuals when a large number of specimens is examined (91 specimens were examined here). The relative width of the hyponotum and pedal sole may also vary due to preservation. Finally, the position of the male aperture was used as a primary feature at supra-generic levels by all past authors (e.g., Hoffmann, 1928, 1929; Labbé, 1934; Starobogatov, 1976). According to Hoffmann (1928, 1929), in *Oncis* (= *Platevindex* + *Semperoncis*, according to Labbé, 1934) and *Onchidium* (= *Paraoncidium* + *Onchidium*, according to Labbé, 1934), the male aperture is below the right tentacle, on its left side (Labbé, 1934), a position that Hoffmann (1928) described as “inside” (*innen* in German); according to Britton (1984), in the same genera, the male aperture is located “in front of the right tentacle.” However, in *Semperoncis montana*, the male aperture is distinctly on the right side of the right tentacle.

The shapes of the radular teeth illustrated here are likely not diagnostic of *Semperoncis montana*. Based on preliminary data obtained from dissections of other onchidiid species (author’s unpublished data), radulae seem to be similar between closely related species, as in many gastropod taxa (e.g., all *Onchidella* species examined so far have similar radulae, which differ from the radulae found in *Peronia* species). However, the fact that SEM pictures of the radula of only three species have been published so far (including the species here) makes it difficult to discuss the variation of the shape of radular teeth. The radular formula varies a great deal among specimens of different sizes: the number of rows ranges from 55 to 75, and the number of teeth per half row ranges from 80 to 150. This information is congruent with other studies illustrating intra-specific radular plasticity and variation in gastropods (e.g.,

Bertsch, 1976; Reid & Mak, 1999; Kawamura et al., 2001), but is of high importance because differences in radular formulae have been traditionally used to distinguish onchidiid species. As for the pattern of intestine loops, used by Labbé (1934) to distinguish genera, Britton (1984) suggested that more than one intestine type could be present in the same species: all specimens dissected here have an intestine of type II. Finally, the rectal gland (only known in *Semperoncis* and *Onchidium* so far), was found in all specimens, regardless of their size.

The male anterior parts (penis and accessory gland) have been the most widely used features to distinguish species and also to delineate genera. However, as was already pointed out by Britton (1984: 180): “No detailed studies of variation have yet been carried out, and in particular, no attempt has been made to assess variation between populations of the same species.” However, the present study, which illustrates ontogenetic changes of onchidiid male parts, raises at least two important points: (1) several species might have been regarded as distinct because mature specimens and immature specimens were being compared; and (2) the study of individual variation should ideally involve immature and mature specimens. The present results are congruent with other gastropod studies on ontogenetic and seasonal changes in genital features (e.g., Smith, 1966; Emberton, 1985; Marcos, 1992).

How many Species of Terrestrial Onchidiids in the Philippines?

When describing *Platevindex apoikistes*, Tillier (1983) found four differences between *montana* and *apoikistes*: (1) the pneumostome is closer to the notum border in *montana*; (2) the genital female aperture is more anterior in *montana*; (3) the notum is more circular and pedal sole proportionally wider in *montana*; (4) and, finally, the penial complex is very small, and a style and a style chamber are absent in *montana*.

The position of the pneumostome on the hyponotum, relative to the notum margin and the lateral side of the pedal sole, varies from about 1/3 to 1/2 close to the pedal sole in the three syntypes of *montana*, which is exactly what was found here in all *apoikistes* type material as well as all additional material. No difference was observed either for the position of the female aperture, located at the posterior end of the peripodial groove, close to the anus. As for the external shape, the description above

includes specimens that are circular, individuals that are wider than long, and individuals that are longer than wide, so the shape of the three syntypes of *montana* fits perfectly within this variation range; the width of the pedal sole of the syntypes of *montana* also fits within the variation of the specimens described above.

The most important feature, however, certainly is the style. Re-examination of the largest syntype of *montana* revealed an important point overlooked by Labbé (1934) and Tillier (1983), that is, this syntype is sexually immature (its female organs are poorly developed). The syntypes of *montana* measure 15 and 18 mm in length, and all individuals examined for the present study measuring less than 20 mm were immature. The male anterior parts of this syntype are identical to the male parts observed in the immature individuals described above (Figs. 33, 34); in particular, the distal end of the accessory gland is a soft papilla instead of a hollow spine (style). As mentioned by Labbé (1934) and Tillier (1983), there is no “style” in the male parts of *montana*, but simply because the syntypes of *montana* are immature. The penis is fully developed and is identical to penises described above, that is, with a solid, proximal stalk, and a distal tube internally covered by minute hooks.

Hence the present study suggests that there is no reason to regard *apoikistes* as a distinct species from *montana*. Therefore, *apoikistes* is to be regarded as a junior synonym of *montana*. Thus, there is only one terrestrial onchidiid species distributed in three Philippine islands (Panay, Sibuyan, and Mindoro), from 150 to 1,850 m in elevation.

Supra-Specific Relationships

The terrestrial onchidiid species redescribed here was referred to as *Oncis montana* by Plate (1893) and Hoffmann (1928), *Semperella montana* by Labbé (1934), and *Platevindex montana* and *Platevindex apoikistes* by Tillier (1983). The specific name that has priority is *montana* Plate, 1893. The next task is to find a generic name.

Unfortunately, the supra-specific relationships within Onchidiidae are largely unclear, and the delineation of genera has remained largely arbitrary (Dayrat, 2009). The species *montana* is placed here in *Semperoncis*, acknowledging that this assignment might very well change in the future. The genus *Semperoncis* was created by Starobogatov (1976), as a replacement name of *Semperella*, which Labbé (1934) created for a few species he wanted to exclude from

Platevindex Baker, 1938 (which he referred to as *Oncis* Plate, 1893).

There are 16 nominal species available in *Platevindex*, six of which might not be valid, and three nominal species available in *Semperoncis* (Dayrat, 2009). All *Platevindex* and *Semperoncis* live in the tropical Indo-West Pacific, and all are marine, with the exception of the three terrestrial species already mentioned.

According to Labbé (1934), a penial gland is absent in *Platevindex* and present in *Semperoncis*. Also, according to Britton (1984), a rectal gland is absent in *Platevindex* and present in *Semperoncis*. For the rest of the diagnosis, *Platevindex* and *Semperoncis* are identical (Labbé, 1934; Britton, 1984): notum with no gills, hyponotum larger or as large as the pedal sole, male aperture below the right ocular tentacle, and asymmetrical kidney. However, none of those features, which are also found in several other genera, such as *Onchidium*, are diagnostic of *Platevindex* and *Semperoncis*. The supra-generic classifications of Starobogatov (1976) and Labbé (1934), although not based on phylogenetics, both suggest that *Semperoncis* and *Platevindex* are close to one another.

In contrast to Labbé (1934) and Britton (1984), Tillier (1983) thought there was no need to distinguish *Semperoncis* (*Semperella*) from *Platevindex*, because nothing was known about the infra- and inter-specific variation of the presence vs. absence of the penial gland, and thus regarded *Semperoncis* (*Semperella*) as a synonym of *Platevindex*. So, *montana* could be classified in *Platevindex sensu lato* (i.e., including species with and without penial and rectal glands) or in *Semperoncis*, a smaller genus restricted to the *Platevindex*-looking species with penial and rectal glands. Until onchidiid genera are delineated using a phylogenetic approach and a broad species sampling, the choice of a genus for *montana* will remain largely arbitrary. *Semperoncis* is selected here for *montana*, mainly because *montana* and *glabra* (type species of *Semperoncis*) do differ from *Platevindex* species by the presence of a penial gland and a male aperture on the right of the right tentacle.

Comments on other *Semperoncis* Species

Semperoncis includes two other nominal species, *S. glabra* (Semper, 1885), the type species, and *S. huberti* Labbé, 1934. Both species are poorly known. *Semperoncis glabra* might be re-described in the future when new

material is available. *Semperoncis huberti* is here regarded as a *nomen dubium*.

Semper originally placed *glabra* in *Onchidium*. It was then transferred to *Oncis* by Plate (1893) where Hoffmann (1928) kept it, and transferred again to the new genus *Semperella* by Labbé (1934), a name replaced by *Semperoncis* by Starobogatov (1976), and, finally, transferred back to *Platevindex* by Tillier (1983). All those new generic assignments took place although no additional material was described.

The five syntypes of *S. glabra* could not be located. Most of Semper's onchidiid types are held by European museums (Berlin, Hamburg, London, Frankfurt), which have all been visited by the author to track onchidiid types, but the type material of *S. glabra* was not found. The type locality of *S. glabra* is "Camiguin de Luzon," a small island North of Luzon Island (~18°56"N, ~121°55"E). Its highest peak is at 790 m, but specimens were apparently not collected on land because the original description does not indicate any terrestrial origin (which is exceptional in onchidiids). In any case, *S. glabra* has always been regarded as a marine species. *S. glabra* is only known from its type locality.

Tillier (1983) referred to a jar containing marine *Platevindex glabra* at the Senckenberg Museum. Indeed, a lot of 10 specimens of *Oncis glabra* was found at this institution (SMF 256161), collected by Möllendorf in or before 1895, from Tablas bei Mindoro, a small island located in between Mindoro, Panay and Sibuyan. Those specimens are externally similar to *Semperoncis montana*. However, this lot is problematic for several reasons: (1) Tablas Island is far from the type locality; (2) more importantly, it is actually not possible to know whether those specimens were collected on land or on the sea shore. According to Ronald Janssen (pers. com.), curator at the Senckenberg Museum, it is more likely that this lot was collected on land because of Möllendorf's personal interests in land snails and slugs (in fact, Möllendorf collected the terrestrial type material of *montana* from Sibuyan). This is supported by the fact that the author of the present contribution found veronicellids in another jar containing onchidiids (identified as *Oncis sp.*) collected by Möllendorf from the "Philippines" with no more geographic or elevation data (SMF 256162). Thus, the lot SMF 256161 at the Senckenberg Museum is likely not a lot of *S. glabra*.

Semper (1885) did provide some information that could indicate that *glabra* and *montana* could, indeed, be closely related: no gills on the dorsal notum, presence of a rectal gland,

penial gland with a distal spine, penis with distal hooks. However, other features seem to indicate that *glabra* and *montana* differ: a penis that measures only 2.5 mm long in *glabra* (penis up to 6 mm in length in *montana*), and a light yellowish dorsal notum (light brown mottled with dark areas in *montana*, or darker). Nevertheless, *glabra* remains poorly known (e.g., radula not described by Semper).

Semperoncis huberti was described by Labbé (1934) based on a single specimen collected from an unknown locality. The holotype could not be located and is likely lost. It is not held by the MNHN (collection visited by the author), where it should be. *Semperoncis huberti* is a poorly known species. Also, because the type locality is unknown, it is very likely that it will remain poorly known for quite some time and is regarded here as a *nomen dubium*. Labbé (1934) did not describe a rectal gland, and it is unclear whether it was just overlooked or really absent. Whether *huberti* should be classified in *Semperoncis* thus remains questionable. In any case, several features seem to indicate that *huberti* differs from both *montana* and *glabra*. The male reproductive organs include a penis similar to the penis described in *montana* and *glabra*, but its length (14 mm) is much longer than in the two other species. Also, the dorsal eyes, for the most part solitary in *montana*, are in groups of two or three in *huberti*. Re-identifying *S. huberti* will remain very difficult, if not impossible, which justifies its status as a *nomen dubium*.

Platevindex ponsonbyi Collinge, 1901, is also poorly-known. It was described based on a single specimen, and in three lines, exclusively based on its color ("dirty green dorsally with large, irregularly black spots. Hyponotum dark greenish-blue; foot-sole dirty yellow.") The holotype could not be located and is likely lost. Several lots of specimens collected from Borneo are held by museums, but they all are marine. It is impossible to decide whether *ponsonbyi* is the same species as *montana*, or a different species.

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LEARNED PREDATOR RECOGNITION IN A FRESHWATER SNAIL, *POMACEA CANALICULATA*

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ABSTRACT

The involvement of associative learning in predator recognition has not been clear in aquatic invertebrates, including molluscs, due to confounding effects of sensitization. The freshwater apple snail, *Pomacea canaliculata*, displays an alarm response (crawling above the water-line) when exposed to crushed conspecifics or some predators. We conducted two series of experiments to investigate whether the apple snail learns to avoid predators. In the first experiment, hatchlings were conditioned simultaneously to crushed conspecifics and either a live carp, *Cyprinus carpio*, or a turtle, *Chinemys reevesii*, and subsequently exposed to the same predator without crushed conspecifics. Irrespective of the predator species used, the alarm response was significantly higher in conditioned snails than in unconditioned snails. Thus, the snail is able to avoid predators by learning, in a broad sense. In the second experiment, designed to distinguish associative learning from sensitization, we conditioned hatchlings to crushed conspecifics and either a carp or a turtle. The hatchlings were subsequently exposed to one or other of the predators. Hatchlings that were conditioned to a predator displayed significantly higher alarm response when later exposed to the same predator than another predator, suggesting that the snail can recognize predators by associative learning.

Key words: alarm response, antipredator defense, apple snail, associative learning, Caenogastropoda.

INTRODUCTION

Prey often alter their behavior in the presence of predators to improve their chances of survival (Kats & Dill, 1998). Such predator-induced alarm responses have been well studied in prey species as they may affect life history strategies, such as changes in growth and reproductive patterns (Crowl & Covich, 1990). Alarm responses may also affect local community structures via trait-mediated indirect interactions (Turner et al., 2000; Trussell et al., 2002).

To survive predation with minimum cost, prey species should exhibit flexibility in their alarm responses, responding to both innate and learned predator cues (Ferrari et al., 2005, 2008). Learning of predator recognition, in the broad sense (i.e., change in behavior in response to experience; Decolmyn, 1998), has been reported in several aquatic animals, including polyclads (Wisenden & Millard, 2001), gastropods (Rochette, 1998; Dalesman et al., 2006; Turner et al., 2006), crustaceans (Hazlett,

2007), insects (Wisenden et al., 1997; Ferrari et al., 2008), fish (Ferrari et al., 2005, 2006, 2007), and amphibians (Ferrari & Chivers, 2008).

However, such behavioral changes may not be caused solely by associative learning between an alarm cue and a specific predator cue. For example, to study predator recognition learning in invertebrates the prey are typically exposed simultaneously to an innate alarm cue, such as injured conspecifics, and a predator cue, such as odor. The response of the prey to the predator cue alone is then tested. This design does not eliminate the possibility of prey sensitization caused by the alarm cue. Sensitization is a simple form of learning in which animals become sensitive to almost any stimulus after they experience a strong noxious stimulus, lasting for several minutes (Decolmyn, 1998) to more than a week (Walters, 1987). In some studies on predator recognition learning, cues that are not used for conditioning are also tested (Wisenden et al., 1997). However, the possibility remains that only the predator cue used in conditioning is strong enough to elicit

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an alarm response after being sensitized. In yet another type of study, the quantity of the innate alarm cue is varied during conditioning to the predator cue. The prey is subsequently shown to respond according to the quantity of the alarm cues used during conditioning (threat-sensitive learning; Ferrari et al., 2008). However, this might indicate that the level of sensitization depends on the quantity of alarm cues. These studies are not intended to distinguish between associative learning and sensitization. However, this distinction is important to support the implications of these studies that prey actually learn to recognize a specific predator rather than that they simply respond to any stimulus above a threshold after being sensitized by the alarm cue. Sensitization in defensive behaviors, such as gill or siphon withdrawal in the marine gastropod *Aplysia*, is a classical example of learning (Decolmyn, 1998) and observed in invertebrates such as gastropods (Walters, 1987; Decolmyn, 1998), crustaceans (Pijanowska et al., 2006), or insects (Walters et al., 2001). Therefore, sensitization is a likely confounding factor in studying predator recognition learning.

Although there are reports in fish (Chivers & Smith, 1994; Ferrari et al., 2005) and amphibians (Ferrari & Chivers, 2008), no study has clearly demonstrated the occurrence of associative learning, instead of sensitization, in predator avoidance in aquatic invertebrates, including molluscs. Associative learning in other behavioral responses has been well documented in molluscs (Alkon, 1999; Hochner et al., 2006), and hence they are likely to use associative learning in predator recognition as well. One method of distinguishing associative learning from sensitization is the use of double conditioning (Chivers & Smith, 1994). This involves the conditioning of two groups of prey individuals to an alarm cue from conspecifics and either of two different predators. The response of the prey to both predators is subsequently observed for each group. In this experimental design, if associative learning is involved, the prey should display a higher intensity of alarm response towards the predator they are conditioned to than towards the other predator. However, if sensitization to the alarm cue occurs, this will raise the intensity of the alarm response in all the treatment groups in a similar way, since all are treated with the same alarm cue.

We evaluated the mechanism of predator recognition in the freshwater apple snail,

Pomacea canaliculata (Caenogastropoda: Ampullariidae), using the double predator conditioning. The apple snail is highly invasive and is now distributed in the Americas and Asia (Joshi & Sebastian, 2006). Hatchlings crawl out of the water when they are exposed to an alarm cue from crushed conspecifics (Ichinose, 2002; Ichinose et al., 2003). However, they also respond to the odours of local predators, such as the climbing perch, *Anabas testudineus*, and the wetland crab, *Esanthelphusa nimoafi*, in non-native areas (Carlsson et al., 2004). This suggests that the apple snail can learn to avoid predators. The ability of learning may be especially important in invasive species that face many novel predators (Hazlett, 2007). In this study, two predators were used, the common carp, *Cyprinus carpio*, and the freshwater turtle *Chinemys reevesii*, both of which are efficient predators of the snail in Japan (Yusa et al., 2006; Yoshie & Yusa, 2008).

MATERIALS AND METHODS

Snails

We collected approximately 100 adult apple snails from paddy fields and canals in Kashiwagi-town, Nara, western Japan (34°40'N, 135°47'E) between July and October 2007. We reared the adults in an aquarium (60 x 30 x 35 cm, *l* x *w* x *h*) containing 60 liters of aerated water at 25–30°C under a natural photoperiod. The snails were fed almost daily with fish food pellets (Hikari Mini Pet, Kyorin, Himeji, Japan). We monitored the aquarium for evidence of egg laying. Each egg mass was transferred to a Petri dish and allowed to hatch at 25°C and under a 14L:10D photoperiod. The hatchlings from each egg mass were transferred to a plastic cylindrical mesh basket (9 cm diameter and 12 cm height) that allowed water exchange but did not allow the snails to escape. We placed the baskets in aquaria (33 x 19 x 21 cm) containing 3 liters of aerated, purified water (chloride, lead, and trihalomethane free). We fed the hatchlings daily with boiled flour balls (~5 mm in diameter; used in Experiment 1 with carp as the predator) or fish food pellets (used in Experiment 1 with turtles and Experiment 2). A preliminary experiment revealed that the type of diet did not affect the number of snails displaying an alarm response to the turtle, either with or without crushed conspecifics ($N = 11$, $F_{1,6} = 0.01\text{--}0.46$; $P = 0.52\text{--}0.92$; ANOVA

with egg mass as a random factor). Juveniles 3–8 days after hatching were used, with no previous experience with predators or crushed conspecifics. Nineteen egg masses were used in the experiments (5–8 for each experimental series), and in most cases, snails from each egg mass were used in all treatment groups.

Predators

We used juvenile carp (1.3–4.8 g) and turtles (5.2–17.4 g). They were obtained from pet shops, except for a carp individual captured from a river in Nara, where the apple snail was not present. Approximately 20 individuals of each species were held in an aquarium (35 x 20 x 25 cm) and acclimated for at least 1 day under the experimental conditions (25°C; 14L:10D photoperiod). The carp were fed tropical fish flakes (Pack de Flakes, Gex, Osaka). The turtles were fed the same diet as the apple snail. Food was withheld for at least 1 day prior to the experiments to avoid the confounding effect of food odour. We used the same predator individual for each replicate throughout the experiment. We attempted to minimize the repeated use of a single individual in each experimental series. However, in some cases it was difficult to identify individual predators over a long period. These animals were reared following the instruction of the Animal Experiment Committee of Nara Women's University.

General Preparation

All experiments were conducted from 08:00–13:00 between August 2007 and April 2008, and each experimental series lasted less than 2 months. One day before the experiment, 10 apple snail hatchlings, from a single egg mass, were taken randomly from the rearing basket and placed in another mesh basket that was held in an aquarium (35 x 20 x 25 cm) containing 5 liters of purified water (5.6 cm deep). The water was aerated and maintained at $25 \pm 1^\circ\text{C}$ throughout the experiment. The snails were supplied with an adequate amount of food and held under a 14L:10D photoperiod. Thirty minutes before the experiment, we removed the food and gently placed all snails that were above the waterline back into the water.

Experiment 1: Conditioning to a Single Predator

There were two experimental series, one using the carp as a predator throughout the

experiment and a second using the turtles. In each series, the experiment was divided into two phases (conditioning and recognition) and the experiment was conducted over a period of 5 days (days 1–5). The hatchlings in each experimental series were divided into two treatment groups (test and control). On day 1, we recorded the number of snails whose bodies were completely out of the water prior to the experiment. We then introduced a single predator (either a carp or a turtle depending on the experimental series) gently into the aquarium, outside the basket. The predator was rinsed with purified water prior to being placed in the aquarium to minimize the possible effect of the rearing water odour (recognition trial). We recorded the number of snails above the waterline 1 h after the experiment began. The duration of the treatment was chosen because the alarm response of the apple snail is highest between 15 min and 1 h (Ichinose et al., 2003), and we wanted to treat the snails with the predator or alarm cues for a long duration. The predator was then removed, the water was changed, and the snails were fed. On day 2 (conditioning trial), we recorded the position of the snails, and then introduced the same predator individual into the aquarium. In addition, we also placed a perforated plastic bag (9.5 x 7.5 cm) containing five crushed hatchlings from the same egg mass as those tested into the aquarium (test treatment). The control treatment consisted of a single predator and an empty bag, without crushed hatchlings. The number of snails above the waterline was recorded 1 h after the introduction of the predator and the bag. At the conclusion of the experiment, we removed the predator and the bag, changed the water, and fed the snails. On days 3 and 5, we repeated the recognition trial (predator only). Dead snails (less than 1% of individuals tested) were removed during the experiment. The experiment was replicated 11 times using the carp, and 14 and 13 times for the test and control treatments, respectively, using the turtle. (One control replicate of the experiment using the turtle was lost because extract from crushed conspecifics was entered by mistake.)

Experiment 2: Double Predator Conditioning

This experiment was divided into two phases (conditioning and recognition trials) over a period of 3 days (days 1–3). On day 1 we conditioned 10 snails in each aquarium to five

crushed conspecifics (also from the same egg mass) and a single predator (either a carp or a turtle). After 1 h we removed the predator and the crushed conspecifics, changed the water, and fed the snails. On day 3 we tested the response of the hatchlings to either a carp or a turtle (recognition trial). Thus, each replicate ($N = 10$ snails) was assigned to one of the following four treatment groups based on the predator used during conditioning/recognition trials: carp/carp (CC), turtle/carp (TC), carp/turtle (CT), and turtle/turtle (TT). There were 8 replicates for the CC, TC, and CT treatments and 7 replicates for the TT treatment (due to the death of a turtle in the TT treatment). We did not use control treatments (no treatment on day 1 and then exposed to each predator on day 3, as in Experiment 1) because our objective was to distinguish associative learning from other components by comparing the above four treatments.

Statistical Tests and Predictions

The number of snails displaying an alarm response was defined as the number of individuals above the water 1 h after the introduction of the predator minus the number prior to the introduction. The intensity of the alarm response was measured by the proportion, that is, the number of snails displaying the alarm response divided by the total number in each replicate ($N = 10$ in most cases). The data were $\log_{10}$ transformed when they violated the assumptions of normality and homoscedasticity, checked by Shapiro-Wilk test and Bartlett test, respectively. All statistical tests were two-tailed, and conducted using JMP IN 5.0 (Sall et al., 2004).

We compared the proportion of individuals displaying an alarm response in Experiment 1 between the test and control treatments. We used one-way ANOVA with the treatment (test or control) as the independent factor, with the egg mass identity added as a random factor (Grafen & Hails, 2002) using the REML option in JMP. By incorporating this random factor, we could statistically control the difference in the alarm response among egg masses or through time (as egg masses were laid over maximum 2 months). We focused the statistical test on the response of snails at the first recognition trial after conditioning (on day 3): if predator avoidance occurs as a result of learning, in the broad sense, a significant difference between the treatments should have been observed on day 3. However, we also studied the difference on

the other days to check the requirements of the experiment (no difference on day 1 and a significant difference on day 2), and the duration of learned predator avoidance as descriptive purposes (on day 5). By focusing the critical test on day 3, we avoided the problems of multiple comparisons and the interdependence of the data over experimental days.

In Experiment 2, we compared the intensity of the alarm response using two-way ANOVA, with the identity of the egg mass added as a random factor. In the recognition trial on day 3, we tested the effect of predator species used (carp or turtle) (termed "predator used"), whether or not the same predator was used in the conditioning and recognition trials ("consistency of the predator"), and the interaction term between them. If associative learning is involved, then "consistency of the predator" should have a significant effect. The "predator used" term reflects the difference in the intensity of immediate response of the snails to each predator. The interaction term corresponds to the effect of predator used in the conditioning trial on day 1, including sensitization to the predator. Note that these effects are not mutually exclusive.

To check the requirements of the experiment, we also tested the effects of "predator used" (on day 1), "consistency of the predator", and their interaction term in the conditioning trial on day 1. The "predator used" tests the immediate response to the predator for the first time (likely to be an innate response), and "consistency of the predator" and the interaction term test if there are pre-existing differences in the alarm response among treatment groups.

RESULTS

Experiment 1: Conditioning to a Single Predator

In the experiments using the carp, there was no difference in the proportion of snails displaying an alarm response between the test and control treatments in the recognition trial on day 1 ($F_{1,15} = 0.13$, $P = 0.73$ after $\log_{10}$ transformation; Fig. 1). In the conditioning trial on day 2, the proportion of snails displaying an alarm response in the test treatment (carp and crushed conspecifics) was significantly higher than in the control treatment (carp only) ($F_{1,15} = 71.52$, $P < 0.001$). Similarly, on day 3, the alarm response in the test treatment group was significantly greater than in the control

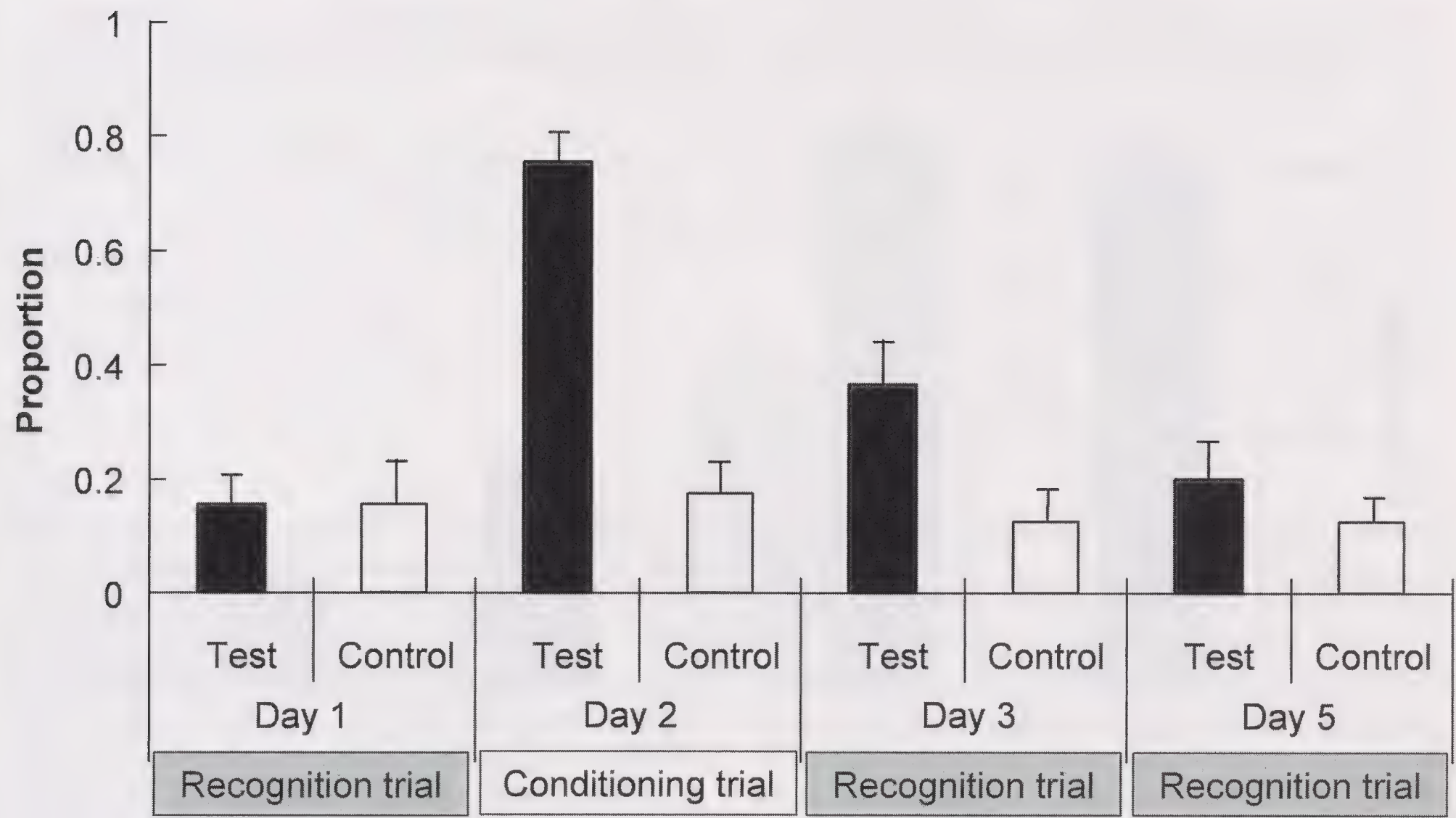


FIG. 1. Proportion (mean + SE) of snails displaying an alarm response in Experiment 1 (carp). Test snails were treated with crushed conspecifics and a live carp on day 2 and with the carp alone on other days, whereas control snails were treated with a live carp alone throughout. N = 11 for both test and control treatments.

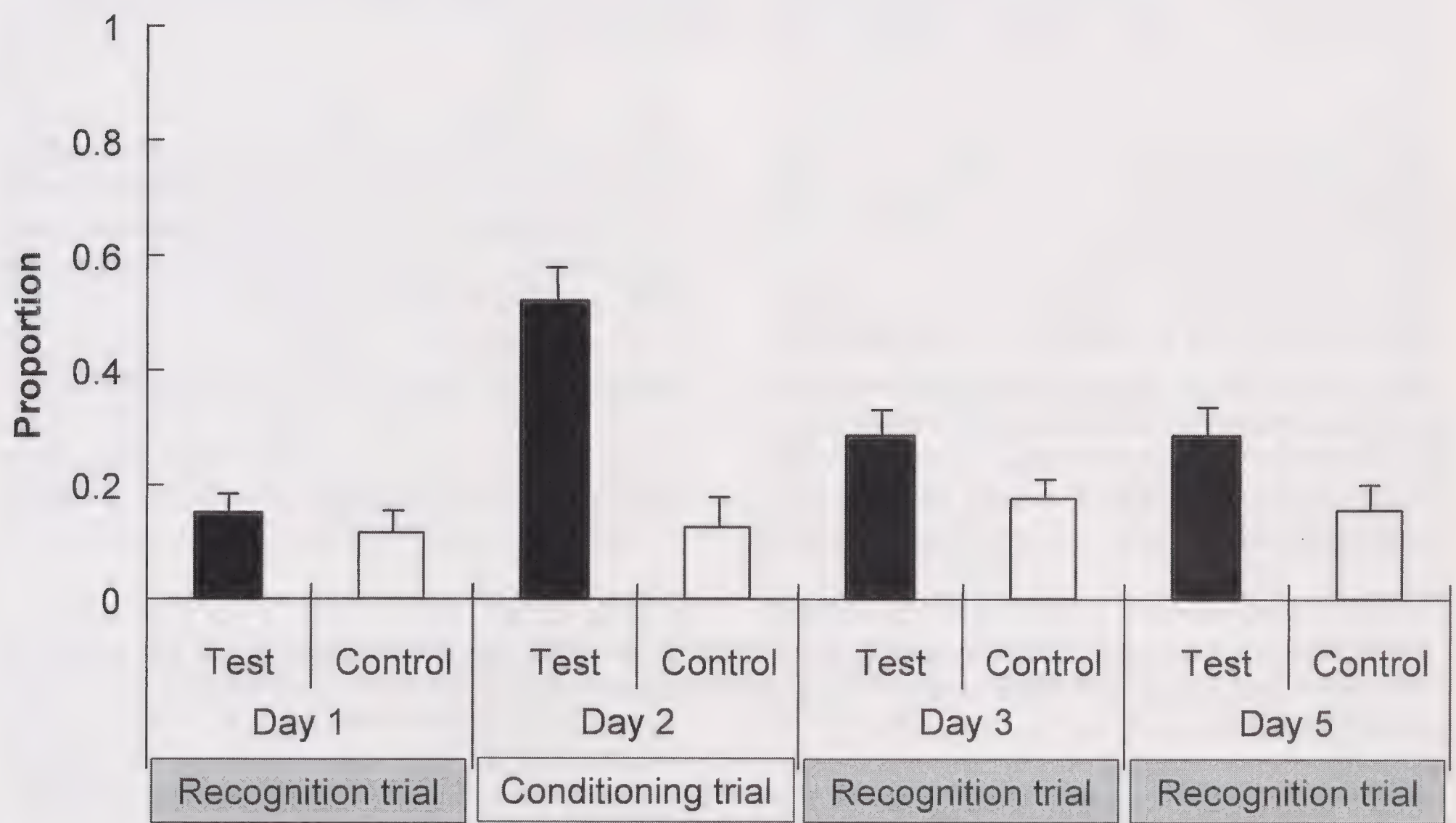


FIG. 2. Proportion (mean + SE) of snails displaying an alarm response in Experiment 1 (turtle). Test snails were treated with crushed conspecifics and a live turtle on day 2 and with the turtle alone on other days, whereas control snails were treated with a live turtle alone throughout. N = 14 for test treatment and N = 13 for control treatment.

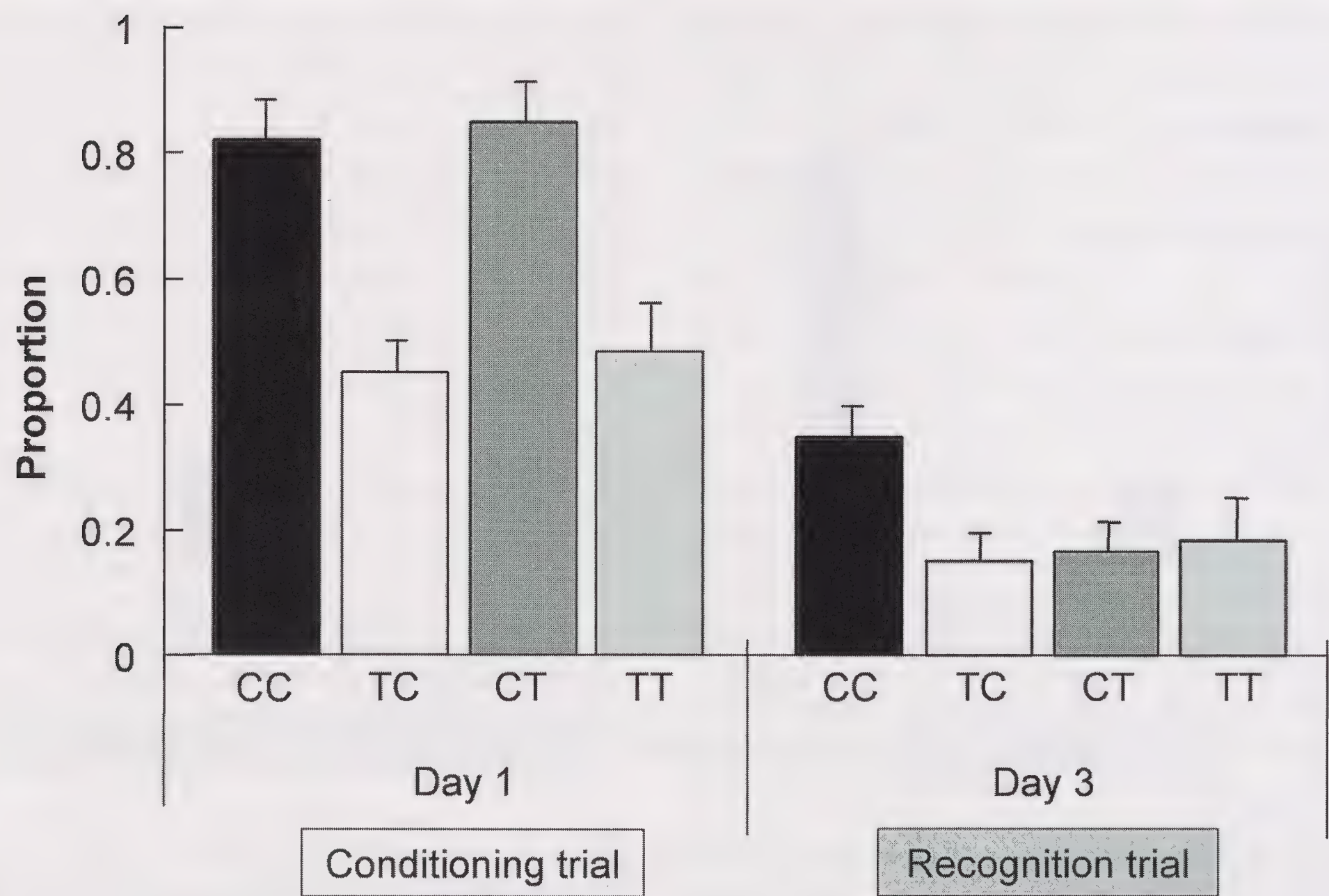


FIG. 3. Proportion (mean + SE) of snails displaying an alarm response in Experiment 2. The first letter in each treatment group indicates the predator used in conditioning with crushed conspecifics on day 1 (carp or turtle), and the second letter indicates the predator used in the recognition trial on day 3. N = 7 for TT treatment and N = 8 for other treatments.

treatment ($F_{1,15} = 8.62, P = 0.010$). There was no significant difference between the test and control groups on day 5 ($F_{1,15} = 1.26, P = 0.28$ after $\log_{10}$ transformation).

In the experiments using the turtle, the pattern was similar to the experiments using the carp. The proportion of snails displaying an alarm response was not different between the test and control treatments in the recognition trial on day 1 ($F_{1,20} = 2.06, P = 0.17$; Fig. 2). The proportion was higher in the test treatment than

in the control during the conditioning trial on day 2 ($F_{1,20} = 27.45, P < 0.001$). The difference was also significant during the recognition trial on day 3 ($F_{1,20} = 4.46, P = 0.047$), but not on day 5 ($F_{1,20} = 3.71, P = 0.066$).

Experiment 2: Double Predator Conditioning

The intensity of the alarm response was high during conditioning to a carp and crushed conspecifics on day 1 (Fig. 3). Between 83 and

TABLE 1. Results of an ANOVA testing the effects of “predator used”, “consistency of the predator” and their interaction term on alarm responses of snails during the conditioning trial (day 1) in Experiment 2.

Source	df	MS	F	P
Predator used on day 1	1	1.0400	40.00	< 0.001
Consistency of the predator	1	0.0004	0.017	0.90
Predator used x Consistency	1	0.0082	0.315	0.58
Error	23	0.0260		

TABLE 2. Results of an ANOVA testing the effects of “predator used”, “consistency of the predator” and their interaction term on alarm responses of snails during the recognition trial (day 3) in Experiment 2.

Source	df	MS	F	P
Predator used on day 3	1	0.0436	2.28	0.140
Consistency of the predator	1	0.0972	5.07	0.034
Predator used x Consistency	1	0.0594	3.10	0.092
Error	23	0.0192		

85% of the snails crawled out of the water in the CC and CT treatments, respectively. The intensity of the alarm response was lower when the snails were conditioned to a turtle and crushed conspecifics (45 and 49% for the TC and the TT treatments, respectively). The results of an ANOVA (Table 1) suggest that the identity of the predator used had a significant effect on the intensity of alarm response. Neither the “consistency of the predator” nor the interaction term had a significant effect (Table 1), suggesting that there was no pre-existing bias prior to the recognition trial.

The snails that had been conditioned to a carp on day 1 and subsequently exposed to a carp on day 3 (the CC treatment) had the highest alarm response (Fig. 3). The next highest was in the TT treatment, followed by the CT and TC treatments, although the difference among these three treatments was small. As a result of an ANOVA, “consistency of the predator” (i.e. whether or not the same predator was used throughout) had a significant effect on the intensity of alarm response on day 3 (Table 2). Effects of the immediate response of snails to the predator used on day 3 and the interaction term were not significant.

DISCUSSION

In Experiment 1, the alarm responses of apple snails to a predator were more intense when the snails had been exposed to both the predator and crushed conspecifics than the predator alone (Figs. 1, 2). The response was independent of the identity of the predator (carp versus turtle). These results indicate that predator avoidance is learned in a broad sense, which includes the possibility of associative learning and sensitization. This learning lasted at least 1 day (up to day 3), but the memory became weakened within 3 days (up to day 5).

Some freshwater pulmonate snails (Dalesman et al., 2006; Turner et al., 2006) and a marine caenogastropod (Rochette et al., 1998) are able to learn to avoid predators. Although there have been no reports regarding learned predator avoidance in freshwater caenogastropods, this study indicates that they are able to learn to avoid predators. Given this, learned predator avoidance may be important to snails in freshwater environments, and probably in marine environments as well.

The results of Experiment 2 indicate that the snails responded with greater intensity when conditioned to both a predator and the crushed conspecifics, then exposed to the same predator, as opposed to another species (“consistency of the predator” in Table 2). This suggests the use of associative learning with respect to a particular predator. We note only one other study with double predator conditioning, conducted in a minnow, *Pimephales promelas* (Chivers & Smith, 1994). However, we exposed conditioned prey individuals only once to one of the predators in the recognition trial unlike the previous study. Using this experimental design and two-way ANOVA, we could statistically distinguish the effect of associative learning (indicated as effect of “consistency of the predator”) from other components such as sensitization. One-way ANOVA followed by multiple comparisons is not the best test, because our hypothesis was the involvement of associative learning in general and not associative learning to each of the predator species.

In general, prey species have various innate and learned components of predator avoidance (Turner et al., 2006; Ferrari et al., 2007, 2008). Therefore, the occurrence of associative learning does not deny the possibility of sensitization or an innately higher response to one predator than another. During the conditioning trial in Experiment 2, when the snails experienced the predators for the first time, the response of

the snails to the carp was significantly greater than to the turtle. This result suggests that the innate response of the snails differed with respect to the identity of the predator, in the presence of crushed conspecifics. We cannot fully exclude the possibility that the odour from crushed conspecifics reached experimental snails more quickly in the carp treatment, if the carp moved more actively than the turtle. However, we think this unlikely, because the tank water was always mixed by the current caused by aeration.

In most reports on learned predator avoidance (e.g., Wisenden & Millard, 2001; Ferrari et al., 2005; Dalesman et al., 2006; Turner et al., 2006; Ferrari et al., 2006, 2007, 2008; Hazlett, 2007), test animals are exposed to the odour of the predator as a stimulus. We used live predators to simulate attack, as did Rochette et al. (1998). Thus, the snails could perceive not only the odours from the predators but also other cues such as their movement. Although this method does not allow conclusions regarding the cues used for predator recognition, it is more realistic of actual predation events in the field (Aizaki & Yusa, 2009). Our method also allows for the possibility that learning requires multiple stimuli, such as chemical and mechanical stimuli, acting together.

In summary, our study has shown that predator recognition in the apple snail has learned components. Among these, associative learning is the most parsimonious explanation. Further studies are required as various innate and learned components interact in a complicated manner to form predator recognition (Turner et al., 2006; Ferrari et al., 2007, 2008).

ACKNOWLEDGEMENTS

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**MACTRA GUIDOI N. SP. AND MACTRA PATAGONICA
(BIVALVIA: MACTRIDAE), TWO LONG MISUNDERSTOOD SPECIES
FROM SOUTHWESTERN ATLANTIC OCEAN**

Javier H. Signorelli^{1*} & Fabrizio Scarabino²

ABSTRACT

A common mactrid from the southwestern Atlantic Ocean has been largely misunderstood in the literature. Since the early 20th century, this species has been referred to as *Mactra patagonica* d'Orbigny, 1846. However, the latter is recorded in Quaternary deposits of Northern Patagonia. ***Mactra guidoi*** n. sp. is described herein, including its shell ultrastructure, hinge features, and soft parts, and compared with the holotype of *M. patagonica*. To compare and to correctly identify both species, a morphometric analysis was carried out using conventional and geometric morphometric methods. ***Mactra guidoi*** n. sp. has an elongate shell that is more fragile than that of *M. patagonica*. In addition, its ventral posterior edge is usually sinuous. The ultrastructure of the shell reveals two layers with cross lamellar structure. The anatomical features agree with those of the congeneric *M. isabelleana*, although they differ in the morphology of the labial palps and foot. Morphometric analysis revealed significant differences between *M. patagonica* and the new species. The relative warp analysis allows us to understand the variation recognized by using CVA. Only *M. patagonica* revealed significant allometry between Relative Warp and Centroid size. Finally, the comparison of the types clearly points towards the existence of two different species.

Key words: *Mactra*, geometric, morphometric, southwestern Atlantic, anatomy.

INTRODUCTION

The cosmopolitan family Mactridae Lamarck, 1809 (Bivalvia: Heterodonta), is well represented in South American waters. The genus *Mactra* Linnaeus, 1767, has been cited from the southwestern Atlantic Ocean by d'Orbigny (1846), among others, when he described four species in his *Voyage dans Amérique Meridionale*. From the Uruguayan and Argentine coasts, he recorded two species: *Mactra isabelleana* (1846: 509; 1847: pl. 77, figs. 25, 26), and *Mactra patagonica* (1846: 507–510; 1847: pl. 77, fig. 27), collected in Maldonado Bay, Uruguay, and the Río Negro province coast, Argentina, respectively (Fig. 1). Several authors have contributed to the knowledge of this group in the literature of the second half of 19th century besides d'Orbigny, describing and discussing many species worldwide, including South America (Dall, 1894, 1897, 1901; Deshayes, 1853, 1854, 1855; Philippi, 1845, 1893a, 1893b; Reeve, 1854, Smith, 1881, 1905, 1914, 1915, among

others). The two main revisions of the taxonomy of mactrid species were by Lamy (1917–1918) and Küster & Weinkauff (1841–1884), who did not analyze the status of *Mactra patagonica*. Later, South American authors have mentioned as *Mactra patagonica* a common morphotype found on these coasts and in Brazil (e.g., Ihering, 1907; Carcelles, 1944; Barattini & Ureta, 1961; Figueiras & Sicardi, 1969; Castellanos, 1970; Rios, 1994). Aguirre (1994) found that this form, incorrectly called *Mactra patagonica* (*non* d'Orbigny, 1846) by Argentinean, Uruguayan and Brazilian authors, differs from the type material of d'Orbigny's species. However, she maintained an open nomenclature, mainly due to the scarce material available. Finally, Scarabino et al. (2006) considered this form to be an undescribed species. During an ongoing revision of the southwestern Atlantic species belonging to the family Mactridae, it became necessary to characterize this frequently mentioned morphotype, describing it as a new species herein called ***Mactra guidoi*** n. sp.

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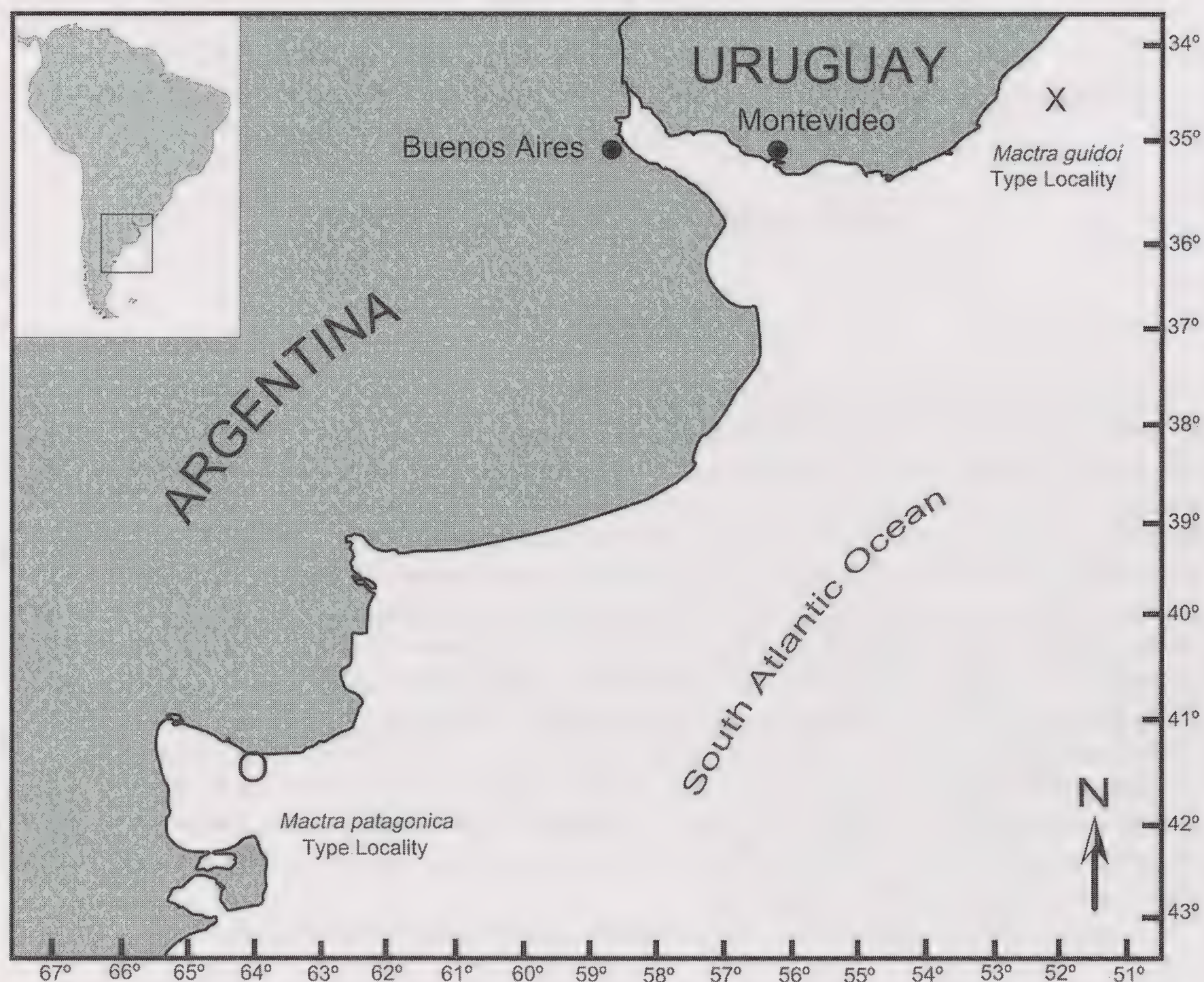


FIG. 1. Map of the study area showing the type localities of *Mactra patagonica* d'Orbigny (○) and *Mactra guidoi* n. sp. (X).

Despite the frequent records of this species, very little live-collected material is available in museum collections. Recent efforts to locate these few lots yielded material that allows this new description. Also, recent collection of *M. patagonica* (d'Orbigny) from the type locality in Río Negro Province, Argentina, enabled comparison of the two taxa.

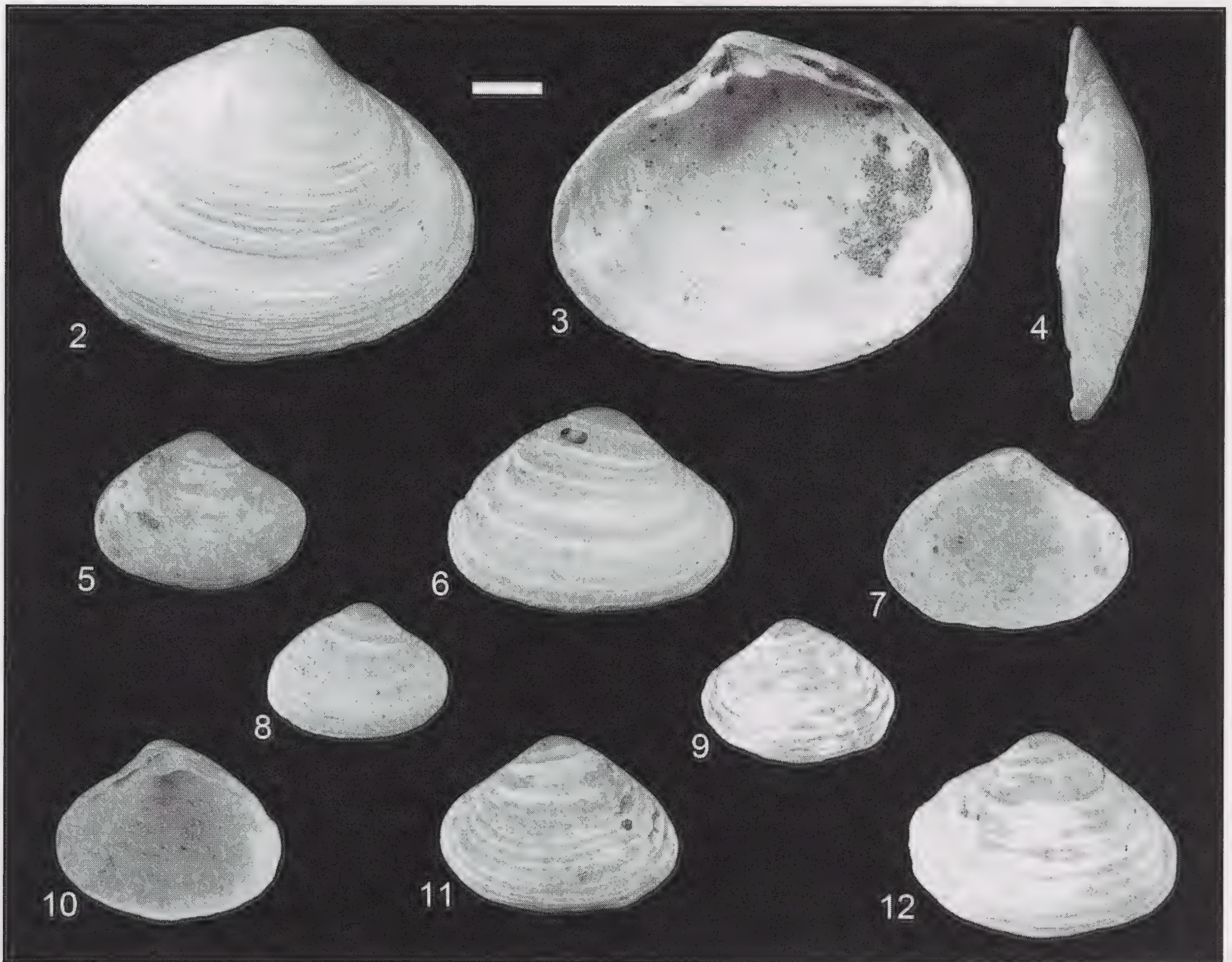
MATERIAL AND METHODS

The collections examined to determinate the distribution of this species are those housed in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) and Museo de la Plata (MLP) in Argentina; Museo Nacional de Historia Natural y Antropología (MNHNM) and Museo Zoológico Municipal "Dámaso A. Larrañaga" (Barattini collection, MZM) in Uruguay; Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Oceanográfico, Fundação Universidade do Rio Grande (FURG), and Museu Nacional de Rio de Janeiro (MNRJ) in Brazil. In

addition, two of the main North American malacological collections [Academy of Natural Sciences of Philadelphia (ANSP) and National Museum of Natural History, Smithsonian Institution (USNM)] were also surveyed. Several field expeditions were conducted on the Uruguayan and Argentine coasts, including the type locality in Río Negro province (Fig. 1), to collect live specimens. The holotype of *Mactra patagonica* d'Orbigny, 1846 (NHM 1854.12.4.668) (Figs. 2–12), was also examined. In this paper, live-collected specimens are indicated as "lv", articulated valves as "av," and single valves as: "sv".

The hinge was described by using the method developed by Bernard and Munier Chalmas (according to Cox, in: Cox et al., 1969). The ultrastructure of the shell was analyzed with a Phillips XL30 scanning electron microscope (SEM). A general description of the soft tissues was done using a *camera lucida* Leica MZ 9.5 and SEM pictures.

To fully characterize the differences between *Mactra patagonica* and *M. guidoi* n. sp., a morphometric study on the shells was carried out.



FIGS. 2–12. *Mactra patagonica* d'Orbigny, 1846. FIGS. 2–4: Holotype, NHM 1854.12.4.668; FIGS. 5–12: Topotypes, (MACN 37570). Scale bar = 1 cm.

Conventional morphometric analysis was done by measuring three parameters with a caliper (length, height and width). Additionally, a geometric morphometric analysis was completed. In the interior side of each left valve 11 Type 1 landmark coordinates (Rohlf, 1996) were recognized from digital images (Fig. 32) by using the software TPSdig2 version 2.05 (Rohlf, 2006). The digitalized data obtained were used to calculate specimen size as centroid size, and to describe the shape. Shape description of was obtained using a principal warp method (RWA), comparable to a Principal Component Analysis, which summarizes a specimen's shape as a deformation from a common reference. This study was performed with tpsRelw (Rohlf, 2005). The difference between species was tested with a multivariate analysis of variance (MANOVA) of partial warp scores and posterior categorization was revealed by using canonical variates analysis (CVA). Statistical analysis was done with Statistica 7.0 for Windows (StatSoft, Inc., 2004).

RESULTS

Superfamily Mactroidea Lamarck, 1809
Family Mactridae Lamarck, 1809
Subfamily Mactrinae Lamarck, 1809
Genus *Mactra* Linnaeus, 1767

Type species: *Cardium stultorum* Linnaeus, 1758; SD Fleming, 1818.

Diagnosis: Trigonal to oval valves, concentrically sculptured, without radial sculpture, subequilateral, inflated, with a brownish periostracum; external ligament separated from the internal by a shelly lamina; lateral teeth smooth; pallial sinus rounded, oval to triangular.

Remarks: The supraspecific systematics of Mactrinae awaits world-wide revision and cladistic analysis. The inclusion of each species here treated in *Mactra* should therefore be considered tentative.

***Mactra guidoi* new species**
(Figs. 13–24)

Mactra patagonica (non d'Orbigny) – Ihering, 1907: 423; Carcelles, 1944: 283, pl. 10, fig. 82; Barattini, 1951: 247; Barattini & Ureta, 1961: 169; Figueiras, 1961: 17; Parodiz, 1962: 42; Richards & Craig, 1963: 137, pl. 2, figs. 7, 8; Figueiras & Sicardi, 1969: 365, pl. IV, fig. 54; Forti Estevez, 1969: 90, pl. 50, fig. 1a, b; 1984: 581, pl. 3, fig. 9a, b; Castellanos, 1970: 235, pl. 21, figs. 1–3; Closs & Forti, 1971: 32, pl. 3, fig. 6a, b. Scarabino, 1977: 210; Figueiras & Sicardi, 1980: 137; Rios, 1966: 33; 1975: 235, pl. 74, fig. 1127; 1985: 243, pl. 86, fig. 1209; 1994: 265, pl. 90, fig. 1291.

Mactra aff. *patagonica* Aguirre, 1994: 138, pl. 1, fig. 12.

Mactra sp. Scarabino et al., 2006: 164.

Type Locality

60 km ENE of Cabo Polonio, Uruguay (34°10'S, 53°04'W; 29 m) collected using a shrimp trawl in 1982 (Fig. 1).

Type Material

Holotype: Articulated valves MNHNM 15526; paratypes MNHNM 15527 (3 sv, 2 av); MACN 37507 (1 av); MNHN 21121 (1 av); FURG 30536 (1 av); USNM 878150 (1 av). All collected in the type locality. MNRJ 9261 (2 lv in alcohol), 23 km Southeast of Chuy, Uruguay (33°52'00"S, 53°10'6"W; 22 m).

Etymology

Named after Dr. Guido Pastorino, advisor and friend of the authors in recognition of his teachings and advice over the years.

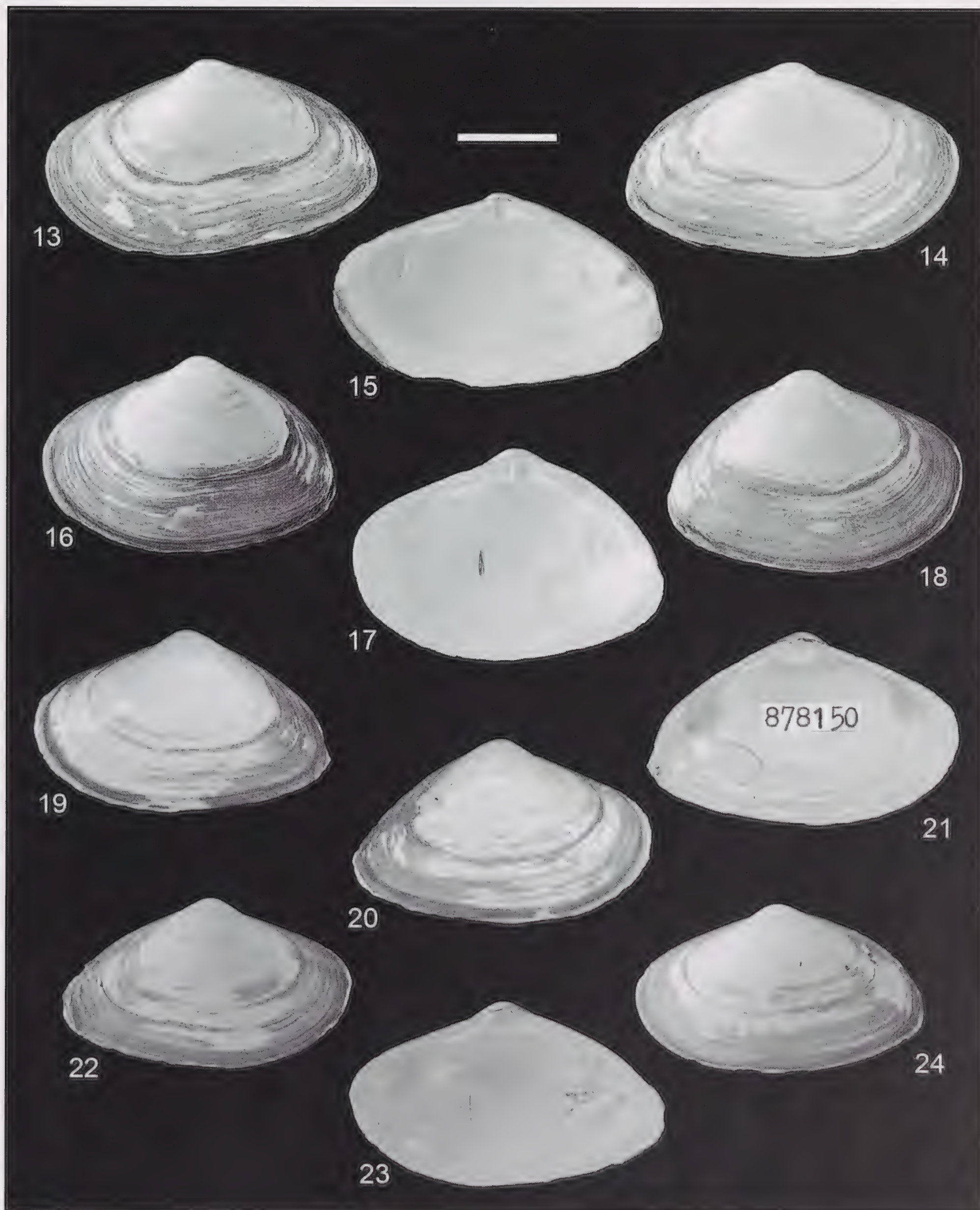
Material Examined

Guarapari, Espírito Santo, Brazil (FURG 14252; MZUSP 77334, 2 sv; MZUSP 77295, 5 sv); Rio de Janeiro, Brazil (USNM 96121, 2 sv; FURG 15056, 8 sv without periostracum; FURG 28169, 3 sv); 48 km SE of São Sebastião, São Paulo, Brazil (MNHNM 8725, col. by L. Tommasi in 1962, 110 m, sand and mud, 21 sv); Porto Belo, Santa Catarina, Brazil (FURG 16532, 6 sv without periostracum); Rio Grande do Sul, Brazil (FURG 32905, 13 av with periostracum); Cassino, Rio Grande do Sul, Brazil (FURG 16420, 1 sv); Chuy, Uruguay (FURG 27088, 18 av with periostracum; FURG 21423, 36 sv with-

out periostracum); 62 km ENE of Cabo Polonio, Uruguay (34°10'S–53°04'W), Uruguay, R/V "Aldebaran", 29 m, fine sand and muddy sand, Spatangue and Piccard dredges (topotypes, MNHNM 15531, 10 av some with remnants of periostracum); 102 km off Cabo Castillos, Rocha, Uruguay, (F/V "Narval"), (MNHNM 2393, col. by J. Alvarez in 1970, 60–70 m, 1 sv); Cabo Polonio, Rocha Uruguay, (MNHNM 8465, 23 m, muddy sand, R/V "Hero", cruise 1972-3^a, station 10, col. in 1972, 43 sv); Cabo Polonio, Rocha, Uruguay (MNHNM 15333, col. by F. Scarabino & I. Pereyra in 2004, 1 sv; MLP 5241, 1 sv); Rocha, Uruguay (FURG 855, 3 sv with periostracum, MZM no number, 7 sv); La Paloma, Uruguay, (MACN 15390, 4 sv; MNHNM 15121 col. by M. Demicheli in 1998, 3 av; MACN 15167, col. by Carcelles, 1 sv; MNHNM 2465. col. in 1962 by J. Olazarri, 1 sv; MNHNM 7335, col. in 1957 by Klappenbach, 5 sv); 80 km S of La Paloma, Rocha, Uruguay, col. by J. Alvarez in 1970, 60 m (F/V "Narval") (MNHNM 4666, 1 sv); Maldonado, Uruguay (ANSP 251819, col. by Pilsbry in 1950, 3 sv; ANSP 251779, col. by Pilsbry in 1950, 2 sv; USNM 347543); Punta del Este, Uruguay (MACN 15189, col. by Carcelles in 1920, 1 sv); Areneras de Carrasco, Canelones, Uruguay (MNHNM 15532, col. by F. Scarabino in 1990, subfossil, 7 sv); Río de la Plata, Argentina (USNM 96165, 1 sv without periostracum); Mar Chiquita, Argentina, (MACN 21203, col. by Doello-Jurado, 4 sv); Mar del Plata, Argentina (MACN 11965, col. by Doello-Jurado in 1920, 50 sv without periostracum, including the valve illustrated in Carcelles 1944: 283, pl. 10 fig. 82; MACN 9361-2, col. by Doello-Jurado, mytilid bank, 20 sv; MACN 8810, 10 sv; MACN 10313, col. by Doello-Jurado in 1920, 20 sv; MACN 8814, Patria sta. 64, 2nd expedition, 8 sv; MACN 8815, Patria sta. 65, 2nd expedition, 10 sv; MACN 8816, Patria sta. 75-76-77, 9 sv; MACN 8817, Patria sta. 79, 3rd expedition, 16 sv); Miramar, Argentina (MACN 8451-8, col. by Doello-Jurado, 4 sv; MACN 9248-1, col. by J. Dupuy, 9 sv; MLP 9376, 1 sv); Quequén, Argentina (MACN 21139, 1 valve); Necochea, Argentina (MLP 3895, 10 sv); Claromecó, Argentina (MLP 1455, 2 sv; MLP 9375, col. by Hylton Scott, 2 sv; MLP 2351, 10 sv); Monte Hermoso, Argentina (ANSP 72644, col. in 1898, 2 sv; USNM 152884, 2 sv; MLP 9382, 2 sv; MLP 9374, 2 sv; MLP 1836, 3 sv; MACN 9210-6, 5 sv); Puerto Militar, Argentina (MNHMM 4009, col. by Fontana in 1919, 10 sv; MACN 6620-4, col. by H. von Ihering, 4 sv; MACN 11187, col. by Doello-Jurado in 1920, 4 sv); Bahía Blanca, Argentina (MACN 24203, col. By Pozzi-Motti in 1939, 23 m depth, 6 sv

without periostracum); Villarino, San Matías Gulf, Argentina (MLP 2758, 7 sv); Patagonia, Argentina (MACN 11434, col. by Sr. Greslebin in 1920, 9 sv; MACN 11689, col. by Sr. Greslebin

in 1920, 9 sv); San Antonio Oeste, Argentina (FURG 16267, 2 av with periostracum); Punta Norte, Valdés Península, Argentina (MACN 11513, col. by Kraglievich in 1920, 14 sv).



FIGS. 13–24. *Mactra guidoi* n. sp. FIGS. 13–15: Holotype, MNHNM 15526; FIGS. 16–24: Paratypes; FIGS. 16–18: MACN 37507; FIGS. 19–21: USNM 878150; FIGS. 22, 23: MNHN 21121; FIG. 24: FURG 30536. Scale bar = 1 cm.

Diagnosis

Shell elongate, moderately stout, elliptical; pallial sinus rounded, short; posteroventral margin usually sinuous; periostracum brownish.

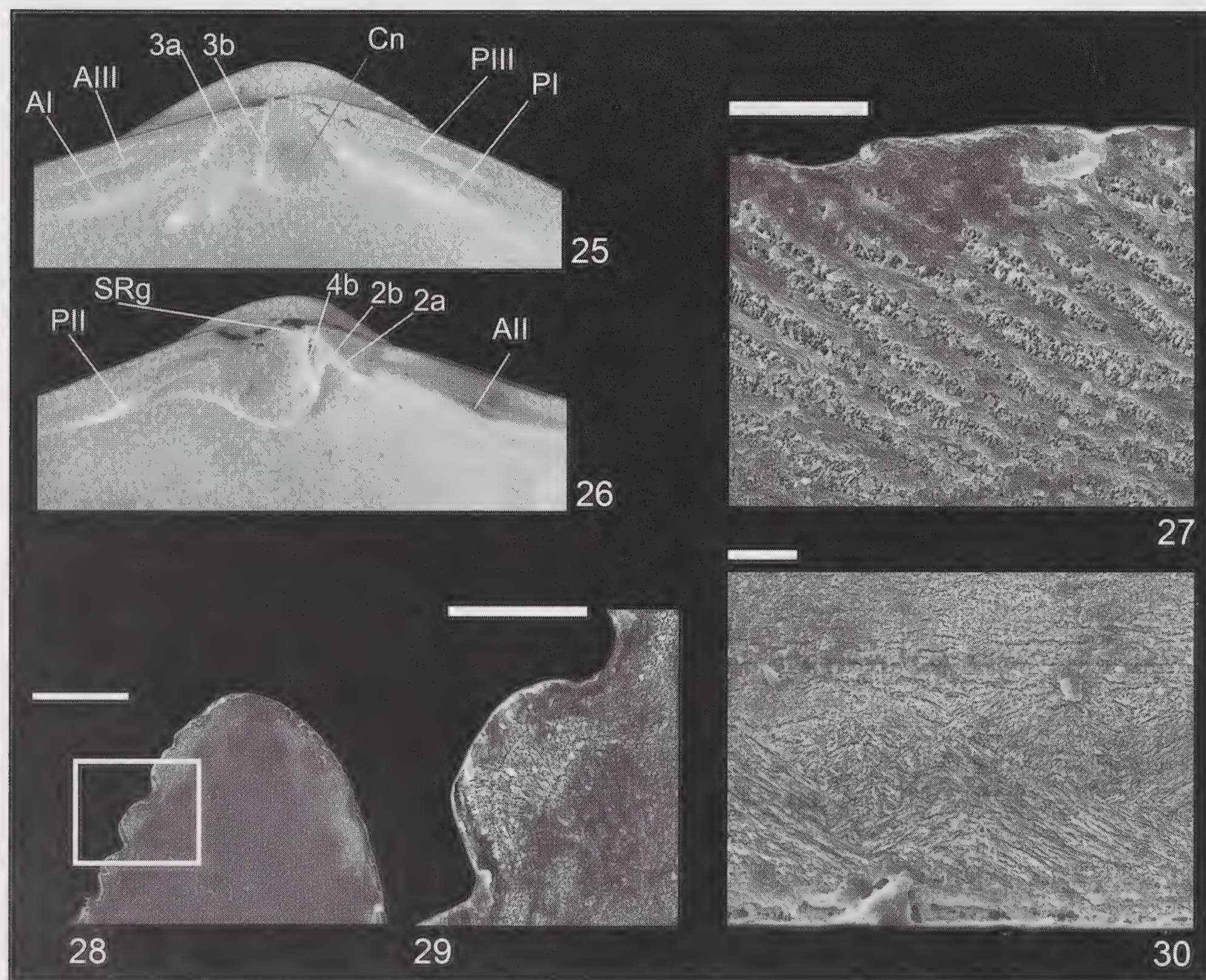
Description

Shell: Up to 45 mm in length, elongate, elliptical, equilateral, with slightly prosogyrate umbo. Posteroventral margin usually sinuated. A weakly defined ridge delineates a posterior area. Lunule not well delineated. Surface smooth, covered by brownish periostracum. Heterodont hinge with small cardinal and lateral teeth in relation with the shell size. In right valve, two anterior (LAI & LAIII) and two posterior (LPI & LPIII) lateral teeth located

close to cardinals, parallel and short, the ventral one being the strongest. Two cardinal teeth, posterior cardinal (3b) oriented dorsoventrally flanking chondrophore; anterior (3a) inclined toward anterior (Figs. 25, 26). In left valve, inverted V-shape tooth formed by two cardinal teeth (2a & 2b), the posterior one flanked by accessory lamellae (4b). Two lateral teeth, one anterior and one posterior, each with only one cusp (LAI & LPII). Cardinal teeth continued by shelly ridge that separates internal ligament (seated in resilifer) from external (small and poorly developed). Hinge formula:

Right valve:	AI	AIII	3a	3b	PI	PIII
Left valve:		AI	2a	2b	4b	AI

Pallial sinus short, rounded, U-shaped. Shell ultrastructure composed of two aragonitic lay-



FIGS. 25–30. Shell of *Mactra guidoi* n. sp. FIGS. 25, 26: Hinge; FIG. 27: Outer cross-lamellar layer, Scale bar = 20 µm; FIGS. 28, 29: Radial section of the inner side of the lateral teeth showing the ultrastructure. Scale bar = 100 µm and 20 µm respectively; FIG. 30: Inner complex cross-lamellar layer. Scale bar = 1,000 µm.

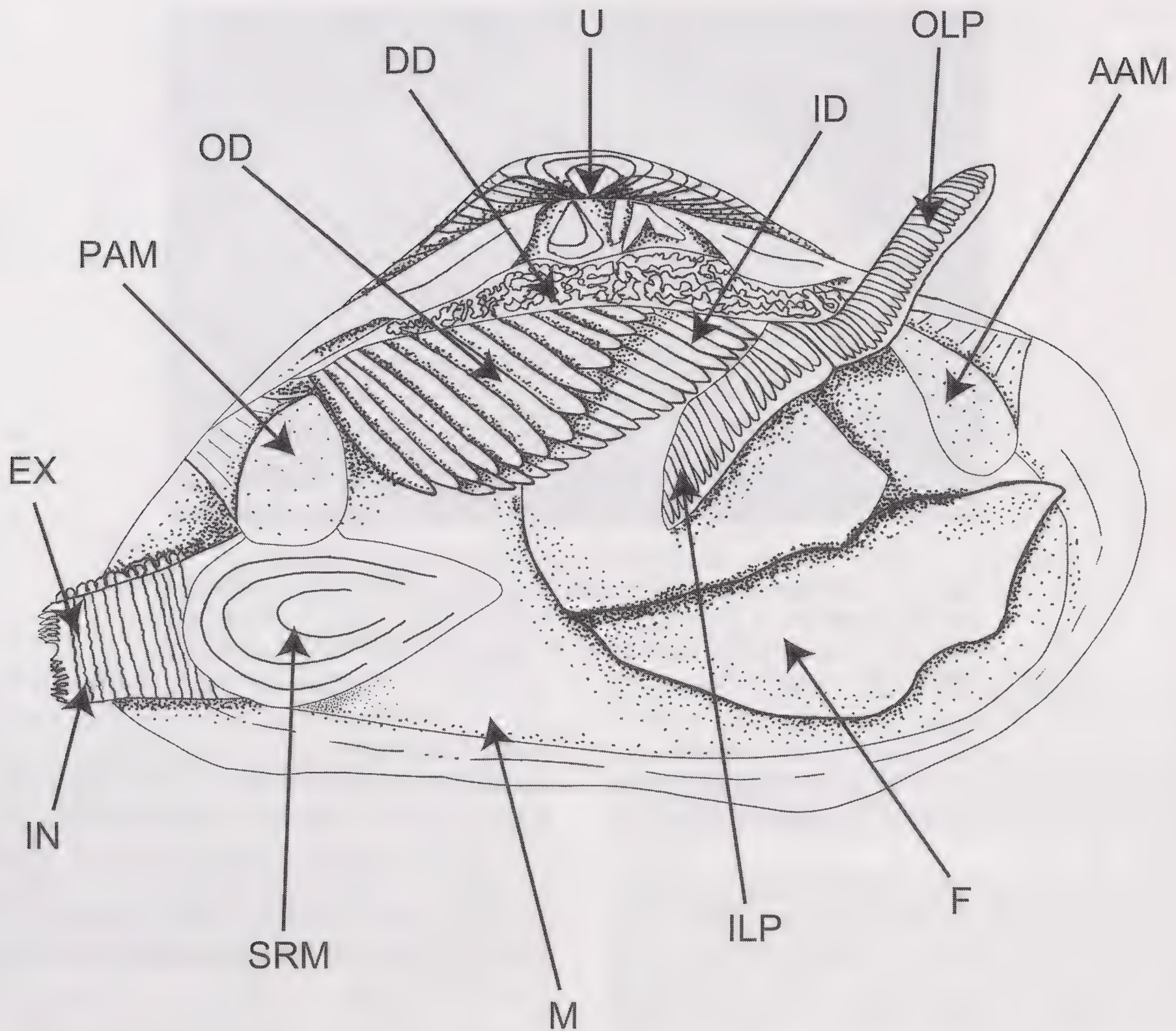


FIG. 31. Anatomy of *Mactra guidoi* n. sp. (AAM, anterior adductor muscle; DD, digestive diverticulum; EX, excurrent siphon; F, foot; ID, inner demibranch; ILP, inner labial palp; IN, incurrent siphon; M, mantle; OD, outer demibranch; OLP, outer labial palp; PAM, posterior adductor muscle; SRM, siphonal retractile muscle; U, umbo) Scale bar = 1 cm.

ers; outer cross-lamellar layer constituted by very thin lamellae; inner layer thinner, with complex cross-lamellar structure (Figs. 27, 30).

Cross-section of dorsal posterior lateral tooth showing radial ultrastructure of internal pustules (Figs. 28, 29) assisting in articulation of lateral teeth. External ligament small, poorly developed, placed in nymph. Internal ligament located in small, ventrally projected chondrophore (Figs. 25, 26).

Anatomy: Adductor muscles large; anterior slightly larger than posterior. Foot laterally compressed, directed anteroventrally. Mantle not fused along ventral edge, but with single point of fusion to form posterior exhalant aperture surrounding siphons (Fig. 31).

Labial palps triangular, very elongate, with inner surfaces plicate and the outer surfaces

smooth. Eulamellibranch ctenidia formed at posterior end, surrounding body, each ctenidium consisting of inner and outer demibranch.

Type C siphons of Yonge (1948), covered completely with periostracum where inner surface of outer mantle fold extends (Fig. 31), representing greatly extended inner surface of outer fold (Yonge, 1957).

Morphometric Analysis: The morphological study of the shells revealed clear differences between the two species. Traditional morphometric analysis demonstrated that the shell of *Mactra patagonica* is more inflated and less elongate than *M. guidoi* n. sp. (Fig. 33). The geometric morphometric method by means of multivariate analysis of variance (MANOVA) revealed significant differences in the shell shape of the two species (Wilks' lambda =

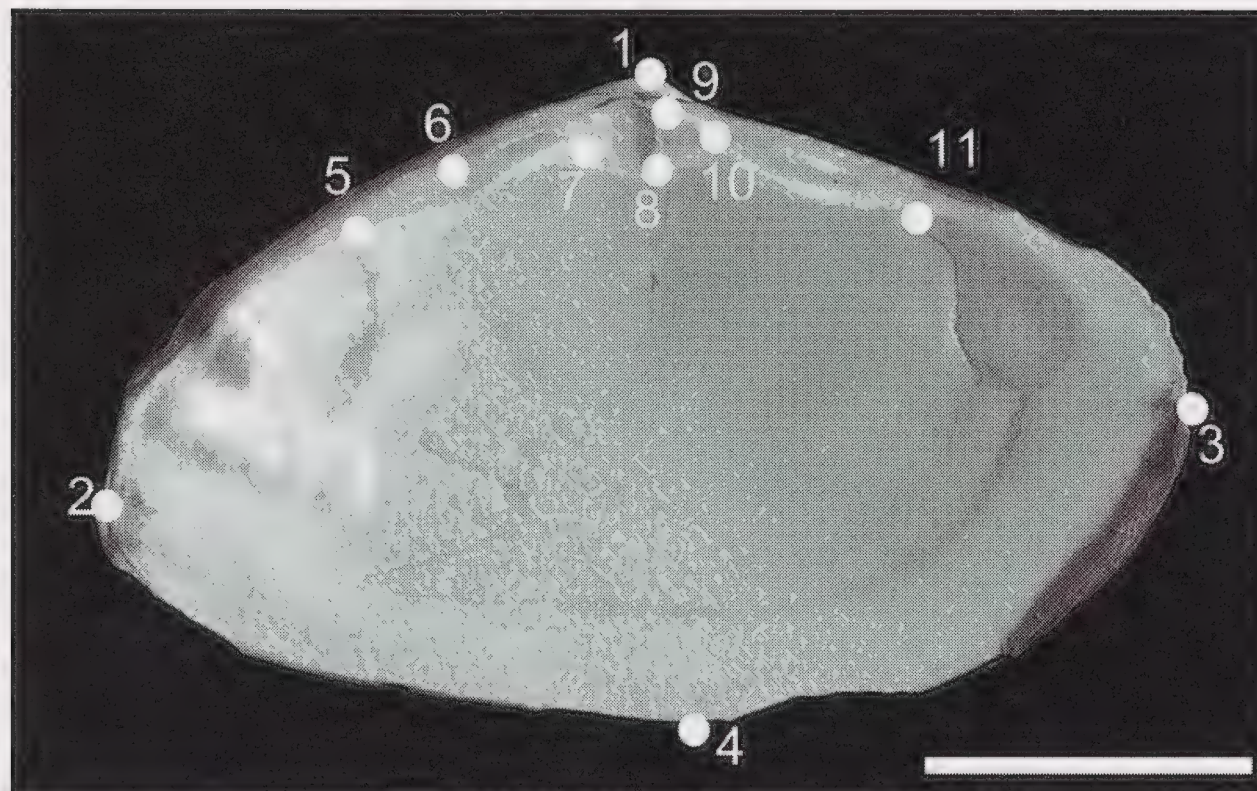


FIG. 32. Internal view of left valve of *Mactra guidoi* n. sp., showing the location of Type I geometrically homologous landmarks. Numbers indicate the order used for digitization of the landmarks. Scale bar = 1 cm.

0.0742; $p < 0.0001$). This differentiation was demonstrated in a Canonical variates analysis (CVA) (Fig. 34).

The RWA allowed understanding the variation recognized by CVA and summarized the descriptions of shape of specimens as linear combinations. The first three RWs explained 76.87% of the variance (RW1 = 53.27%, RW2 = 12.25%, and RW3 = 11.35%) (Fig. 34). To infer the origin of the variation, a test between RWs and centroid size was performed (Fig. 35). The two taxa did not differ significantly in centroid size distribution (ANOVA: $F = 1.686$, $p = 0.20$). In the analysis between RW and

centroid size, only the first relative warp showed significant correlation (Pearson's $r^2 = 0.337$, $p = 0.025$). Linear regression was tested in each taxon. However, only *Mactra patagonica* revealed significant allometry between RW and centroid size (Linear Regression: $r^2 = 0.359$, $p = 0.014$).

Distribution and Ecological Remarks

According to the material examined, *Mactra guidoi* n. sp. can be found in sandy and muddy sand sediments from Espírito Santo, Brazil, to the Valdés Peninsula, Argentina. Valves with

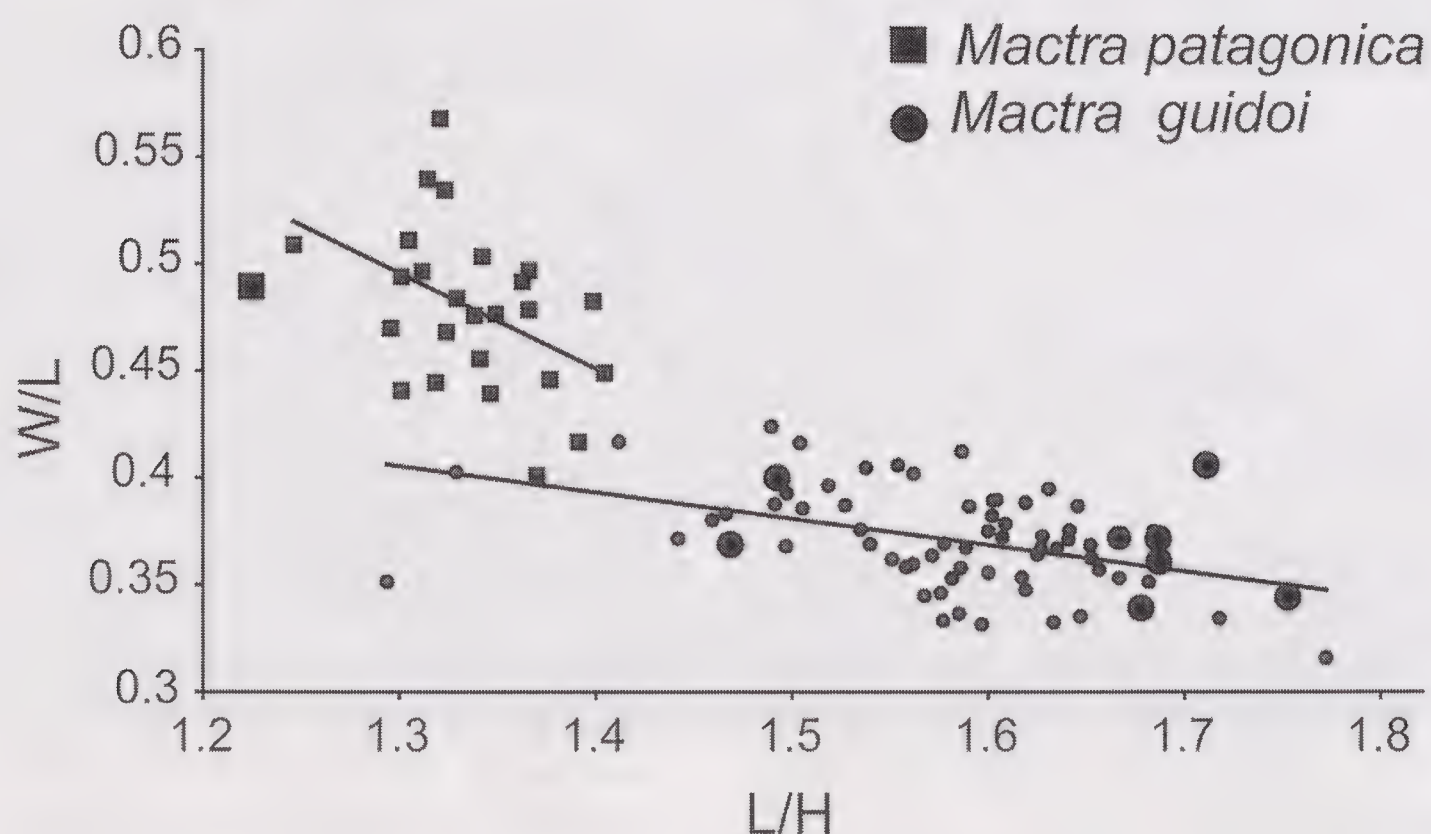


FIG. 33. Traditional morphometric analysis. Relation width/length vs. length/height. Types indicated by large symbols.

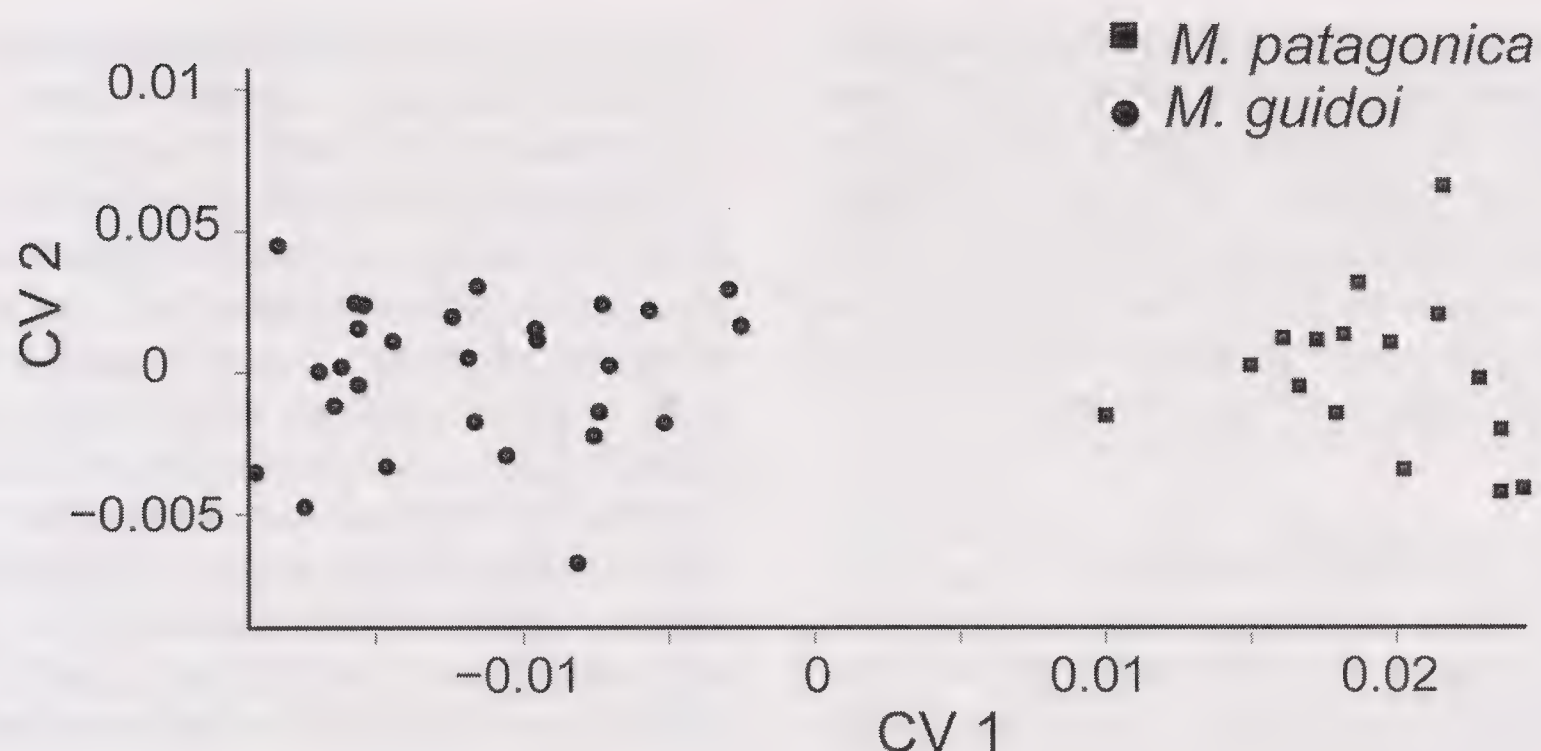


FIG. 34. Canonical variates analysis showing the morphometric variation between *Mactra patagonica* (full squares) and *Mactra guidoi* n. sp. (full circles).

periostracum have been obtained between 20 and 50 m. However, the real depth distribution of living specimens could be more restricted. Live-collected specimens are scarce in all examined collections, but isolated valves are very abundant along the coasts of southern Brazil, Uruguay, and northern Argentina. Scarabino et al. (2006) stressed the contrast between these large number of valves and the few living records, postulating either a population decline and/or the high potential of preservation of the valves. In fact, most components of these beach shell accumulations show a subfossil aspect and most likely come from Holocene deposits.

The type series as well as many valves examined show clear evidence of infestation by

a spionid polychaete, that is, blisters formed in the posterior end in large specimens (Figs. 23, 24) and in the middle of the valve in smaller shells. Boring made by naticids have been also noticed in the umbonal area of several valves.

Mactra guidoi n. sp. is relatively common in Quaternary deposits of southern Brazil, Uruguay, and northern Argentina and was cited as *Mactra patagonica* (e.g., Figueiras, 1961; Parodiz, 1962; Closs & Forti, 1969).

Remarks

The first mention of *Mactra guidoi* n. sp. in Uruguayan Quaternary deposits was by Figueiras (1962), when he also introduced the

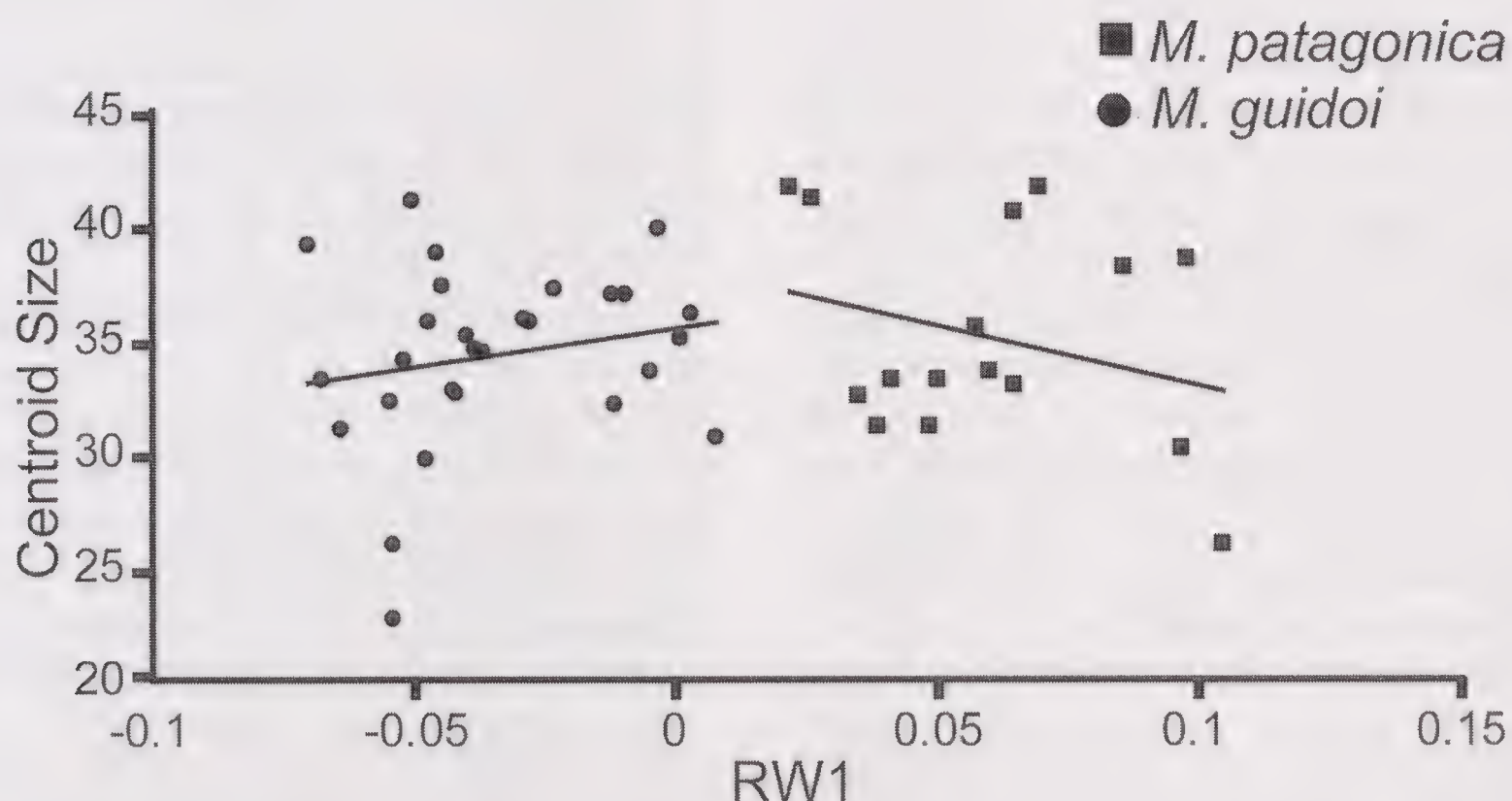


FIG. 35. Allometric curves derived from the relationship between RW 1 and CS. *Mactra patagonica* (full squares) and *Mactra guidoi* n. sp. (full circles).

question about the possible synonymy with *M. duboisi* Doello-Jurado (a *nomen nudum*) cited by de Mata (1947). Examination of a lot from Mar del Plata, Argentina, in Barattini's collection (MZM), with an old label possibly written by Doello-Jurado or Felippone, indicates that *M. duboisi* is a name *in schedula* for *Macra marplatensis* Doello-Jurado, 1949.

DISCUSSION

The holotype of *Macra patagonica* (Figs. 2–4), collected by d'Orbigny from Quaternary deposits in Río Negro Province, clearly differs from the specimens of *M. guidoi* n. sp. (Figs. 13–15). The topotypic specimens of *M. patagonica* illustrated (Figs. 5–12) are smaller compared with the holotype. However, other specimens collected at the type locality were similar in size. These were broken shell specimens and for this reason were not illustrated. In addition, a complete survey of museum material of *M. patagonica* and *M. guidoi* n. sp. in several institutions allowed us establish that the former was only recorded as a fossil from Quaternary deposits. This species is similar in shape to the Recent *M. isabelleana* d'Orbigny, 1846, but the systematic relationship between two taxa is not studied in this paper. *Macra guidoi* n. sp. was collected as a Quaternary subfossil as well as live material.

Recognition of two morphologically distinct species lay hidden for many years. Aguirre (1994) was the first in mentioning this divergence, but left the nomenclatural problem unresolved, a misunderstanding that we were able to track back to Ihering (1907). A specimen in the MACN collection (6620-4) with a label written by Ihering clearly belongs to *M. guidoi* n. sp. In the following decades, Doello-Jurado and Carcelles worked in the MACN collections, and also continued this misidentification. Carcelles (1944) illustrated *M. guidoi* n. sp. as *M. patagonica*, and since then, other authors have repeated the misconception. The obvious differences between species led us to conclude that none of these authors examined the type material collected by d'Orbigny and housed in The Natural History Museum, London. Although several authors (e.g., Figueiras, 1961) did not illustrate the materials attributed to *M. patagonica*, they also had the same misconception of this species, which has been omnipresent on labels and in the literature since Carcelles (1944). Only Feruglio (1933), who collected

material in deposits similar to those of d'Orbigny in North Patagonia, properly cited the species described by the French author.

Two contrasting morphotypes are commonly found in Atlantic waters of southern Brazil, Uruguay, and northern Argentina, one belonging to *Macra isabelleana* (up to 70 mm) and the other to *M. guidoi* n. sp. (up to 45 mm). In general, *M. patagonica* could be included in the first group. Searching for an explanation of the misconception of Ihering, we found three likely causes acting together. The shape of the drawing of *M. patagonica* by d'Orbigny (1846) has some differences but broadly matches that of the type material. However, given the sizes of the drawings of the three *Macra* illustrated on his plate, Ihering would have had the impression that *M. patagonica* was smaller than *M. isabelleana* and similar in size to *M. petiti* d'Orbigny, 1846 (p. 509; 1847: pl. 77, figs. 23, 24), as is in fact *M. guidoi* n. sp. Those differences, however, are not the case, and the measurements indicated in the text by d'Orbigny are 60, 39 and 30 mm long respectively. Secondly, d'Orbigny referred *M. patagonica* as being "bien plus ovale, plus comprimée, et sa forme est différente" than that of *M. isabelleana*, a comparison which also applies (even more so) to *M. guidoi* n. sp. Finally, Ihering probably was under the impression that d'Orbigny found and described the two most common mactrid shells of the coast of southern Uruguay and northern Argentina.

Shell ultrastructure basically agrees with previous studies of other mactrids (Taylor et al., 1973). The scarce material with soft tissues did not allow a detailed anatomical study. However, the gross morphology illustrated here provides a preliminary comparison with the congeneric *M. isabelleana*. The anatomical characters of *M. guidoi* n. sp. differ from those of *M. isabelleana* in having more elongate labial palps and a larger foot in relation to the entire body. The ctenidia are similar and so are the siphons (Type C of Yonge, 1948).

Morphometric analysis revealed and quantified the differences between *M. patagonica* and *M. guidoi* n. sp. Whereas traditional morphometry was sufficient to distinguish the two taxa, geometric morphometric method allowed us to quantify that difference. The species described by d'Orbigny has strong valves with well-developed teeth. *Macra guidoi* n. sp. is more elongate and fragile.

Correction of this nomenclatural problem emphasizes the significance of re-examining type material.

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RE-EVALUATION OF TAXONOMIC CHARACTERS OF *IDIOSEPIUS* (CEPHALOPODA, MOLLUSCA)

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ABSTRACT

Members of the cephalopod genus *Idiosepius* Steenstrup, 1881, are currently mainly identified based on the arrangement of suckers on the tentacular club (i.e., in two or four transverse rows) and the number of suckers on the male hectocotylized ventral arms, as stated by Nesis (1982). However, the discovery of a further species, *I. thailandicus*, raises questions about the validity of the present systematic characters. Alternative morphological features, such as the mantle length and peg arrangement on the tentacle suckers, were proposed by Chotiyaputta et al. (1991) to be suitable for species classification.

To determine whether these attributes are more reliable diagnostic characters valid for all *Idiosepius* species, we re-evaluate all the above taxonomic characters as well as others features, such as the number of suckers on the other extremities, the shape of the hectocotyli, radula morphology, and beak size.

Based on the present analysis, the systematic positions of *I. macrocheir* and *I. thailandicus* are uncertain, although they both correspond morphologically to *I. biserialis*.

The current evaluation supports a revision of the systematic key of Nesis (1982). The data presented here indicate that the species should be characterized by the shape of the hectocotylus and its appendages rather their sucker number. All other evaluated morphological attributes – sucker and its peg arrangement, mantle size, beak and number of suckers in the first three arm pairs – do not provide good characters to discriminate the species of *Idiosepius*.

Key words: classification, hectocotylus, Idiosepiidae, morphology, revision, species characterization, systematic key.

INTRODUCTION

Members of the genus *Idiosepius* Steenstrup, 1881, are the smallest of all cephalopods, with adult mantle lengths of less than 3 cm in females and 1 cm in males (Hylleberg & Nateewathana, 1991 a). One conspicuous morphological character in representatives of this monogeneric family (Idiosepiidae Appellöf, 1898) is the adhesive organ (also known as adhesive gland) located on the posterior portion of the dorsal mantle (Sasaki, 1921; Steenstrup, 1881). Studies on this genus deal with this cephalopod's behavior and development, as well as the morphology of the adhesive organ (Nabhitabhata, 1998; Shigeno & Yamamoto, 2002; Byern et al., 2008). The relationships among species within this family, however, are still unknown.

Jereb & Roper (2005) currently place eight species within the genus *Idiosepius*: *Idiosepius*

biserialis Voss, 1962; *I. macrocheir* Voss, 1962; *I. minimus* (d'Orbigny, 1845); *I. notoides* Berry, 1921b; *I. paradoxus* (Ortmann, 1888); *I. picteti* (Joubin, 1894); *I. pygmaeus* Steenstrup, 1881; and *I. thailandicus* Chotiyaputta et al., 1991. These species are mostly distributed in the tropical Indo-Pacific, Japan, southern Australia, including Tasmania and African waters, but one was found in cooler Russian and Japanese waters (Nesis et al., 2002; Sato et al., 2009). Within the genus, *I. biserialis* has the widest geographical distribution, ranging from Japan to the Indo-Pacific, including Thailand and Indonesia (Byern et al., 2005; Voss, 1963); it has also been recorded in Mozambique (incorrectly annotated by Voss in 1962 as "South Africa").

Nesis (1982) characterized the species of this genus by the arrangement of suckers on their tentacular club (*I. biserialis* with two rows, *I. notoides*, *I. macrocheir*, *I. paradoxus*, *I. picteti*

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and *I. pygmaeus* with four rows) and the number of suckers on the male hectocotylus. However, in his systematic key, only six of the above-mentioned eight species are represented; *Idiosepius thailandicus* was described later by Chotiyaputta et al. (1991). For *I. minimus*, no type material or any detailed morphological descriptions are available to confirming its validity. Nevertheless, this species is mentioned in previous (Berry, 1921a, b) and recent discussions (Jereb & Roper, 2005) of this genus.

The discovery of *I. thailandicus* raises questions about the validity of the above-mentioned systematic characters; this species closely resembles *I. biserialis*, likewise collected by Hylleberg & Nateewathana (1991a) in Thai waters, in having a biserial arrangement of suckers on the tentacle clubs and similar number of suckers on the ventral arms. Chotiyaputta et al. (1991) proposed to differentiate these species by mantle length (*I. thailandicus* slightly smaller than *I. biserialis*) and sucker ultrastructure. Whereas *I. thailandicus* tentacle suckers have two series of pegs that become triple at the distal portion of the club, *I. biserialis* shows a distinct threefold circular arrangement of pegs throughout on the suckers.

To date, however, it remains unverified whether these morphological features (mantle length and sucker ultrastructure) are reliable characters for species other than *I. biserialis* and *I. thailandicus*.

To address this problem, we re-evaluate all taxonomic characters proposed by Nesis (1982) and Chotiyaputta et al. (1991) in all nominal *Idiosepius* species and compare these features against each other. Additionally, we evaluate the suitability of the number of suckers on the other extremities as well the shape of the hectocotyli, radula morphology and beak size.

The purpose of this study is to define easily detectable but reliable morphological characters suitable to classify all nominal species (except *I. minimus*) of the genus *Idiosepius*, and here we aim to contribute to the taxonomic understanding of the pygmy squids, but we also rely on the support of colleagues working on this genus to help us re-organize the systematic key of *Idiosepius*.

MATERIAL AND METHODS

Some of the data presented here are already partially mentioned in the original literature. Those original data are mainly based on a small sample size from one locality.

Samples

All samples presented here were collected by the first author with the help of local partners and with official national collection permissions. In most cases, numerous individuals of species obtained from different localities were likewise evaluated. The number of individuals of each taxon is listed in Tables 1–6.

In order to provide a more complete survey, data of Chotiyaputta et al. (1991), Joubin (1894), Tracey et al. (2003) and Voss (1962) were included when necessary.

Type Material

Re-examination of all type material, apart from *I. macrocheir* (SAM A6521) and *I. picteti* (M 3/75 747/27), was not possible because of the risk of damaging the unique material. Attempts to re-collect these species in their original type locations were unsuccessful: only specimens of *I. pygmaeus hebereri*, collected by Grimpe (1931), could be collected at the original locality by Byern & Klepal (2007). The collected specimens were examined and identified according to the systematic key of Nesis (1982) as well as the original reference literature.

Morphological Analysis

Live specimens were kept in seawater tanks and fed ad libitum with mysids and shrimps. For all collected specimens, mating behavior and egg spawning in aquaculture were observed during sample collection and cultivation, indicating that all animals included in this study were mature. For the subsequent analyses, the animals were anesthetized with 3% ethanol-seawater (v/v) solution, measured, and decapitated.

The body measurements include mantle length, mantle width, and mantle width index, according to Roper & Voss (1983). Measurement of the arm and tentacle length was inappropriate because the appendages were retracted. The mantle with its adhesive organ was isolated and fixed for other investigations (Byern et al., 2008); the head was fixed in 70% EtOH. Some specimens of *I. biserialis* from Mozambique and *I. pygmaeus* from Indonesia were not anesthetized or measured, but were immersed directly in 70% EtOH.

Of each collection place, some individuals of each species were kept intact and given to the collection of the Natural History Museum Vienna (Table 1), but not evaluated in the

TABLE 1. Specimen and collection information for *Idiosepius* spp. (*Museum abbreviations according to Integrated Taxonomic Information System-ITIS; # in the collection of the Muséum d'Histoire Naturelle, Genève, Switzerland, instead of the Musee Oceanographique, Monaco; + re-numbered and stored in the PMBC since 2009).

Species	Location	Coll. Date	Reference	Mus. Ref. No.*
<i>I. biserialis</i>	San Jose Mission Station, Morrumbene, Mozambique (Holotype)	June 1954	Voss, 1962	SAM A6520
	Bang Rong, Phuket Island, Thailand (8°02.156'N; 98°25.487'E)	April 2004		NMW 1032228-103229
	Inhaca Island, Mozambique (26°00.215'S; 32°54.721'E)	October 2004	Byern et al., 2008	NMW 103265-103268
	Inhambane Bay, Mozambique (23°51.184'S; 35°22.553'E)			
	Ekas-Bay, Lombok, Indonesia (08°52.020'S; 116°27.541'E)	May 2004	Byern et al., 2005	-
<i>I. macrocheir</i>	Takasu, Japan	August 2000		-
	Linga Linga, Morrumbene, Mozambique (Holotype)	June 1954	Voss, 1962	SAM A6521
	Vilanculos, Mozambique	May 1973		SAM 186
<i>I. notoides</i>	Goolwa, South Australia (Holotype)		Berry, 1921a	SAMA D17495
	Fortescue Bay, Tasmania Australia (43°08'S; 147°57'E)	May-June 2000	Tracey et al., 2003	-
	Margate, Tasmania, Australia (43°02.969'S; 147°16.034'E)	February 2006	Byern (unpubl. data)	-
	Snug, Tasmania, Australia (43°04.357'S; 147°15.943'E)			
	Katsiyama, Bay of Tokyo, Japan (Holoytpe)		Ortmann, 1888	MZS Mol 5809
<i>I. paradoxus</i>	Nagoya, Japan (34°43.021'N; 136°58.208'E)	April 2005	Byern et al., 2008	NMW 103227, 103273, 103274
	Ushimado, Japan (34°35.567'N; 134°07.340'E)			
	Amboine Island, Indonesia (Holotype)		Joubin, 1894	MHNG M 3/75 747/27#
<i>I. picteti</i>	Zamboanga, Philippines (4°20'N; 107°20'E) (Syntypes)		Steenstrup, 1881	ZMUC CEP-52
	Mudong, Phuket Island, Thailand (7°48.107'N; 98°24.472'E)		Byern et al., 2008	NMW 103230
	Bang Rong, Phuket Island, Thailand (8°02.945'N; 98°25.030'E)	April 2004	Suwanmala et al., 2006	NMW 103231
	Ekas-Bay, Lombok Island, Indonesia (08°52.020'S; 116°27.541'E)	May 2004	Byern et al., 2007	NMW 103223-103225
	Lombok Island, Indonesia (Holotype)	April 1927	Grimpe, 1931	ZMB Moll. 86118a
<i>I. pyg. hebereri</i>	Donsak Surat-tani, Thailand (Lectotype)	May 1989	Chotiyaputta et al., 1991	PMBC 25267+
<i>I. thailandicus</i>	Donsak Surat-tani, Thailand (Paratype)			NSMT Mo 69624 No. 4

present analyses. Most samples are still in the private collection of the first author.

All suckers on the arms and tentacles of the EtOH-fixed specimens were counted using a stereomicroscope (limited to 10 individuals of each sex, species and location). If sucker cups were missing, then sucker pedicels were used to determine their position and these were included in the sucker counts.

The peg arrangement on the suckers – five individuals of each sex/species and from different locations – was examined on different parts (basal, middle and near the tip) of all arms and tentacle clubs. A full statistical evaluation of the pegs of all suckers on arms and tentacles could not be undertaken, the unfavorable position of the differently orientated and the often sediment-occluded suckers preventing complete examinations. Moreover, the length of arms or tentacles could not be measured because of their contraction due to anesthesia and fixation.

For scanning electron microscopic (SEM) analyses, arms, and tentacles were dehydrated in a graded series of ethanol, washed several times in acetone, immersed in HMDS (hexamethyldisilazane), dried overnight in air, mounted on stubs, coated with gold in a Polaron 5800 sputter coater, and examined using a Philips XL 20 SEM.

Beaks were isolated by enzymatic digestion with collagenase IV (Cat #17104-019, Invitrogen, Carlsbad, California, USA) (100 units/ml with phosphate buffer solution, pH 7.4, plus 10% sucrose, shaken for 3–5 days at 37°C). Remaining tissue was removed manually; complete beaks were washed with Aqua bidest and immersed briefly in 1% osmium tetroxide to harden the chitin. Beak dimensions were measured using a dissecting microscope to 0.1 mm accuracy using the software program Lucia 5.10 (Co. Laboratory Imaging, Czech Republic). Measurements taken in all species include upper and lower hood length (UHL, LHL), upper and lower rostral tip to wing base (URW, LRW), upper and lower crest length (UCL, LCL) and lower baseline length (LBL), as defined by Clarke (1962, 1986).

Radulae were isolated by trypsin digestion (0.3% trypsin with 0.15% sodium sulphide for 24 h at 37°C), washed in Aqua bidest, immersed for 24 h in 1% osmium tetroxide, washed again, immersed in HMDS, and further treated for SEM analysis in the same manner as described above for the arms and tentacles.

Characterization of the adhesive organ (Cyran et al., 2005) and of its glandular composition (Byern et al., 2008) as well as reports on the

internal morphology in *I. biserialis* and *I. pygmaeus* (Hylleberg & Nateewathana, 1991a, b) provide no species-related differences.

Statistical representation of results includes means and standard error of means. The 95% confidence intervals of the means were calculated by adding to or subtracting from the mean the standard error of the mean times the theoretically expected t-value ($df = n-1$).

Statistical analysis of ANOVA and Mann Whitney U test was performed with the computer program SPSS (Version 18).

RESULTS

External Morphology

Apart from the commonly known body deformations due to the fixation process, anesthesia also influences the sucker arrangement on the tentacles (but not the arms) of *I. biserialis*, but not that of four-row species. In the anaesthetized state, the tentacle club of *I. biserialis* exhibits the so-far-described two-row arrangement (Fig. 1A), whereas the clubs in non-anaesthetized specimens widen and display a three to four-row sucker arrangement (Fig. 1B, C).

The sucker arrangement of the tentacle club of the female paratype of *I. macrocheir* (Fig. 1D) from the South African Museum (SAM 186) appears to be similarly widened and displays a three-row arrangement.

Mantle Length

Culturing animals for a short time (up to 7–10 days) did not influence the size of *I. biserialis*, *I. paradoxus* or *I. pygmaeus*; the animals kept their size during this cultivation period. Figure 2 and Table 2 provide a detailed overview of size values in all *Idiosepius* species.

Within *Idiosepius biserialis* specimens from Mozambique and Thailand are intermediate in size, in contrast to the larger individuals from Japan and the smaller specimens from Indonesia.

Recent measurements of the holotype of *Idiosepius macrocheir* (SAM A6521) differ slightly from the data of Voss (1962) (original data given in brackets).

Idiosepius notoides from different locations shows size differences. Specimens from Coles Bay, collected by Tracey et al. (2003), are slightly larger than those from Fortescue Bay but bigger than individuals collected by the first author from Snug/Margate.

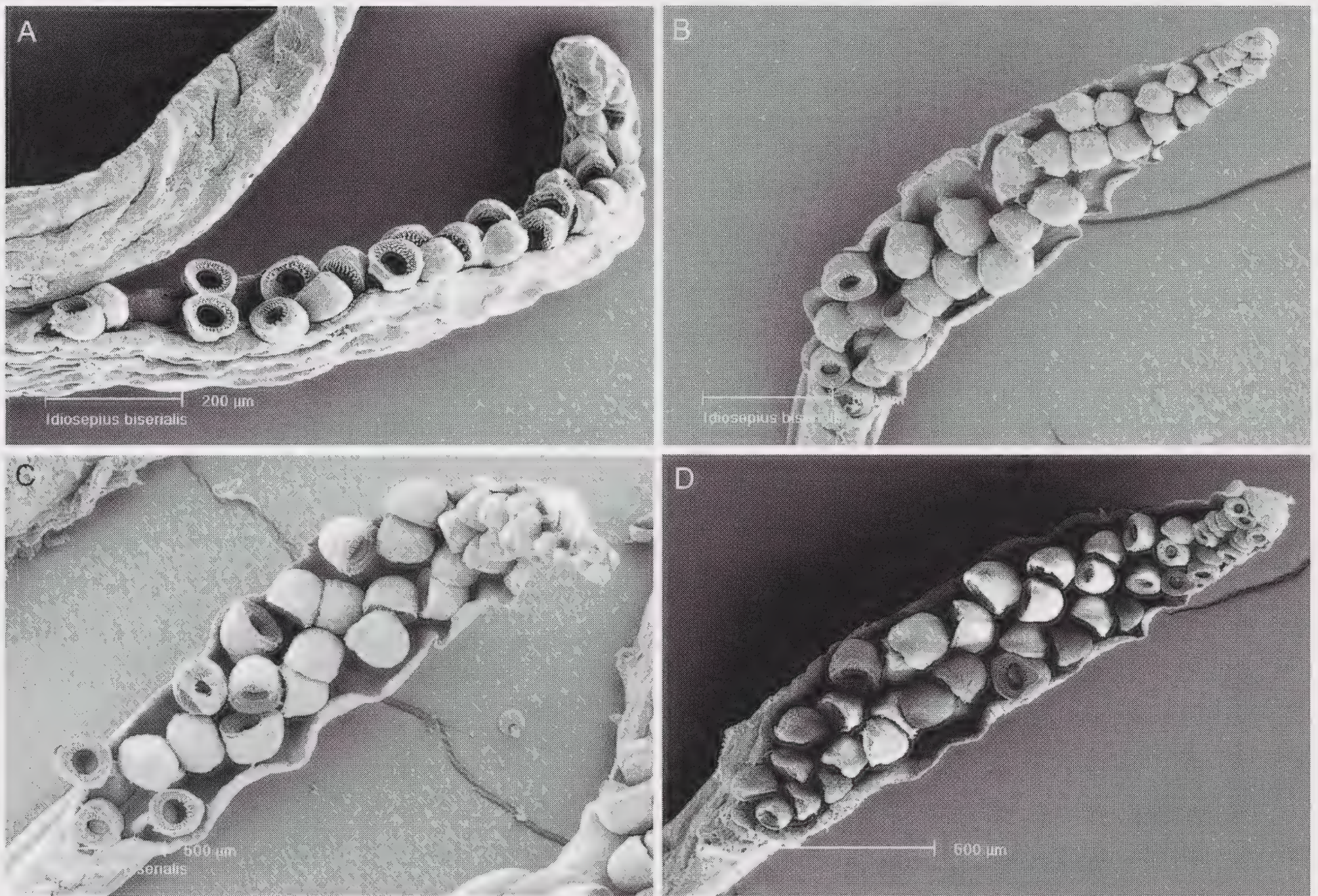


FIG. 1. Suckers of specimens of *Idiosepius biserialis*. (A): 2-rowed arrangement of suckers on the tentacle club; (B, C): 3- up to 4-rowed sucker arrangement; (D): Tentacle club of a female paratype (SAM No. 186) of *I. macrocheir* from the South African Museum.

Individuals of *Idiosepius paradoxus* from Ushimado are smaller than specimens from Nagoya.

The single holotype individual of *Idiosepius picteti* represents the largest male individual within the genus (Joubin, 1894).

The males of *Idiosepius pygmaeus* from Bangrong are almost the same size as those from Mudong. In contrast, a great size difference is apparent in the females from the two locations. Specimens from Bangrong are smaller than those from Mudong. Specimens from Indonesia are similar in size to individuals from Thailand.

Based on the data by Chotiyaputta et al. (1991), the individuals of *Idiosepius thailandicus* are larger than *I. biserialis* from Thailand.

Based on the present mantle length data, females are, regardless their geographical location and species, significantly larger than males, as pointed out in Table 3.

In summary, the results show that both sexes of the two-row species *I. biserialis* (♂ 5.60 mm $\pm$ 0.58 mm; ♀ 7.46 mm $\pm$ 1.04 mm) are

smaller than those of the four-row species *I. notoides*, *I. paradoxus*, *I. pygmaeus* (♂ 11.18 mm $\pm$ 1.53 mm; ♀ 14.32 mm $\pm$ 2.50 mm), whereas females are always almost 1/4–1/3 larger than males.

According to the mantle length, the single female of *I. macrocheir* (10.2 mm) lies between both groups, while *I. picteti* (14 mm) is clearly related to the four-row group.

Suckers on Extremities

Within an individual, each pair of arms and tentacles has a similar number of suckers (Table 4). On average, arm pair II has more suckers than arm pairs III or I. In males, arm pair IV is markedly hectocotylized and has fewer suckers, whereas in females the number of suckers on this arm pair is similar to the other arm pairs. On average, females have more suckers on the tentacle clubs than males. In the following, the total number of suckers on both tentacle clubs of all individuals within each species is used for comparison (Fig. 3).

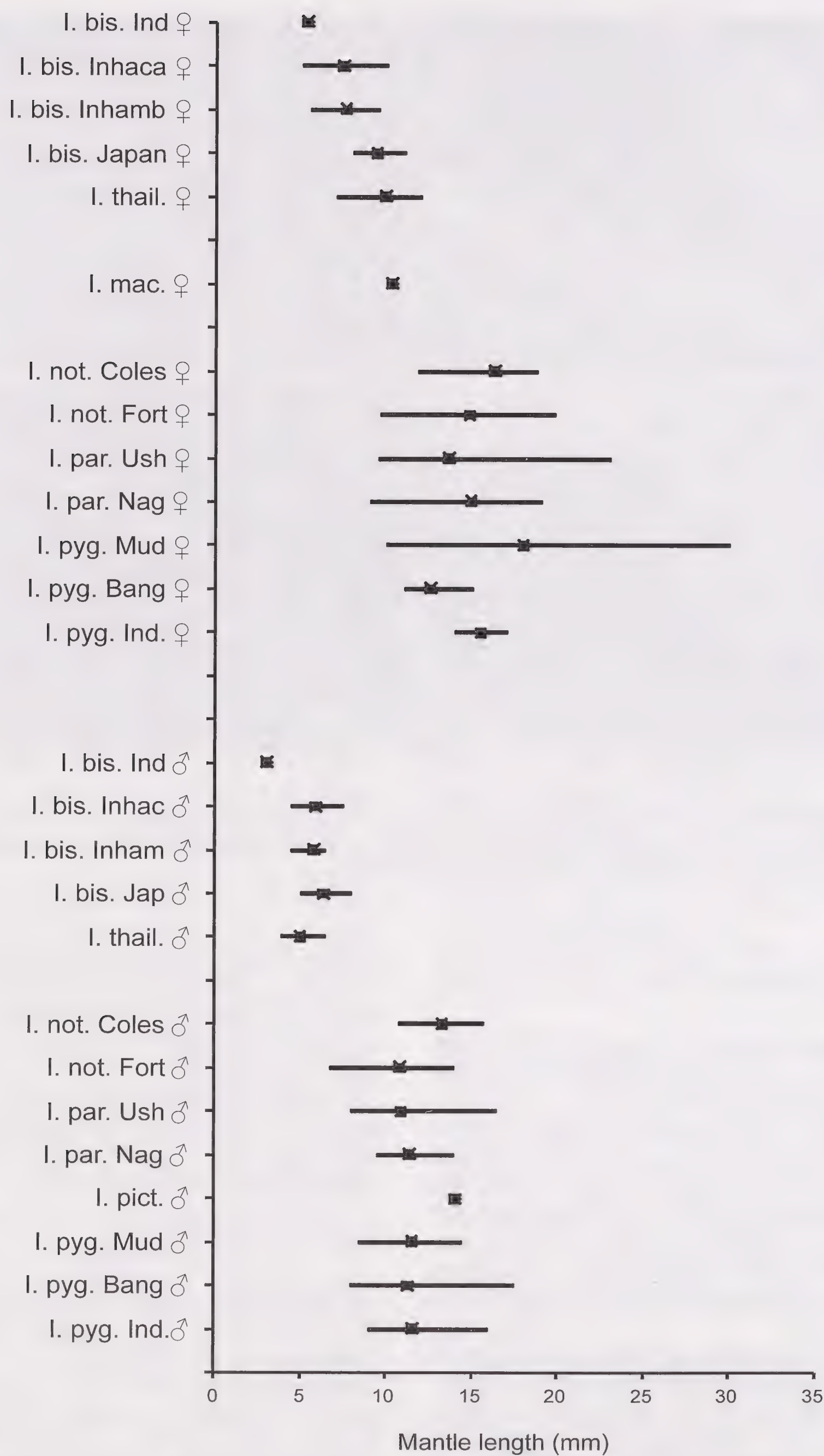


FIG. 2. Mean (■) and 95% confidence interval (n-1) (—) for the mantle length in all *Idiosepius* spp. For some species only a single specimen was available (*I. biserialis* Ind. ♂, *I. macrocheir* ♀ and *I. picteti* ♀), while in other specimens (*I. bis.* Indonesia ♀, *I.pyg.* Indonesia ♀, *I.pyg.* Bangrong ♀) the sample range was low (see Table 2).

TABLE 2. Size measurements in *Idiosepius* spp. specimens studied (■Data by Voss, 1962; +Data by Tracey et al., 2003; #Data by Joubin, 1894; *Data by Chotiyaputta et al., 1991).

Species	Mantle length (mm)		Mantle width (mm)		Mantle width index	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
<i>I. biserialis</i> ♀ Inhaca, Moçambique (n = 39)	7.38	1.31	4.09	0.63	56.16	8.11
<i>I. biserialis</i> ♂ Inhaca, Moçambique (n = 65)	5.84	0.54	3.24	0.34	55.74	6.12
<i>I. biserialis</i> ♀ Inhambane, Moçambique (n = 10)	7.60	1.33	4.15	1.36	54.63	15.74
<i>I. biserialis</i> ♂ Inhambane, Moçambique (n = 24)	5.71	0.57	3.02	0.10	53.37	5.02
<i>I. biserialis</i> ♀ Phuket Island, Thailand (n = 10)	7.70	1.10	4.20	0.80	55.10	3.50
<i>I. biserialis</i> ♂ Phuket Island, Thailand (n = 7)	4.50	0.30	2.20	0.20	48.90	4.60
<i>I. biserialis</i> ♀ Takasu, Japan (n = 4)	9.39	1.10	4.24	0.39	45.29	3.42
<i>I. biserialis</i> ♂ Takasu, Japan (n = 7)	6.34	0.89	3.06	0.50	48.46	6.27
<i>I. biserialis</i> ♀ Lombok, Indonesia (n = 2)	5.25	0.35	4.00	1.41	75.45	21.86
<i>I. biserialis</i> ♂ Lombok, Indonesia (n = 1)	3.00	-	2.50	-	83.33	-
Mean (♀)	7.46	1.04				
Mean (♂)	5.60	0.58				
<i>I. macrocheir</i> ♀ (n = 1) ■	10.20 (10.50)	-	5.32 (6.00)	-	52.16 (57.14)	-
<i>I. notoides</i> ♀ Coles Bay (n = 19)+	16.23	1.69	-	-	-	-
<i>I. notoides</i> ♂ Coles Bay (n = 38)+	13.30	1.20	-	-	-	-
<i>I. notoides</i> ♀ Fortescue Bay (n = 10)+	14.82	3.15	-	-	-	-
<i>I. notoides</i> ♂ Fortescue Bay (n = 14)+	10.78	2.13	-	-	-	-
<i>I. notoides</i> ♀ Snug/Margate (n = 8)	9.06	1.82	6.19	0.75	69.27	6.59
<i>I. notoides</i> ♂ Snug/Margate (n = 18)	8.67	1.90	5.86	0.74	69.57	11.06
Mean (♀)	13.37	2.22				
Mean (♂)	10.92	1.74				
<i>I. paradoxus</i> ♀ Ushimado, Japan (n = 27)	13.54	2.60	7.06	1.07	53.05	8.76
<i>I. paradoxus</i> ♂ Ushimado, Japan (n = 83)	10.93	1.32	5.4	0.66	49.78	6.36
<i>I. paradoxus</i> ♀ Nagoya, Japan (n = 23)	14.93	2.42	7.63	0.90	52.97	14.57
<i>I. paradoxus</i> ♂ Nagoya, Japan (n = 34)	11.37	1.01	5.53	0.63	48.88	6.27
Mean (♀)	14.24	2.51				
Mean (♂)	11.15	1.17				
<i>I. picteti</i> ♂ (n = 1)#	14.00	-	5.50	-	39.29	-
<i>I. pygmaeus</i> ♀ Mudong (n = 15)	17.97	4.04	8.53	1.14	48.40	6.33
<i>I. pygmaeus</i> ♂ Mudong (n = 89)	11.58	1.19	5.01	0.65	43.40	5.00
<i>I. pygmaeus</i> ♀ Bangrong (n = 3)	12.50	2.18	6.33	1.04	51.74	12.70
<i>I. pygmaeus</i> ♂ Bangrong (n = 25)	11.28	2.10	4.82	1.06	42.81	6.14
<i>I. pygmaeus</i> ♀ Lombok (n = 2)	15.50	2.12	7.50	2.12	47.90	7.13
<i>I. pygmaeus</i> ♂ Lombok (n = 42)	11.57	1.28	5.49	0.70	47.82	6.12
Mean (♀)	15.32	2.78				
Mean (♂)	11.46	1.55				
<i>I. thailandicus</i> ♀ (n = 13)*	9.85	-	5.72	-	58.10	-
<i>I. thailandicus</i> ♂ (n = 11)*	5.03	-	2.96	-	58.90	-

TABLE 3. Sexual dimorphism of mantle lengths in *Idiosepius* spp. Females are, regardless their geographical location and species, significantly larger than males.

Species	Model	df	F	Sig.
<i>I. biserialis</i> ♀ = 59 ♂ = 96	Corrected Model	1	131.737	0.000
	Intercept	1	7404.771	0.000
	Sex	1	131.737	0.000
<i>I. notoides</i> ♀ = 37 ♂ = 70	Corrected Model	1	20.374	0.000
	Intercept	1	1885.277	0.000
	Sex	1	20.374	0.000
<i>I. paradoxus</i> ♀ = 50 ♂ = 117	Corrected Model	1	110.088	0.000
	Intercept	1	7208.160	0.000
	Sex	1	110.088	0.000
<i>I. pygmaeus</i> ♀ = 18 ♂ = 56	Corrected Model	1	136.184	0.000
	Intercept	1	3642.924	0.000
	Sex	1	136.184	0.000

Idiosepius biserialis has 39.5 ± 5.09 (♀) and 32.11 ± 2.93 (♂) suckers on the clubs; males from Japan have more suckers on tentacles than animals from Thailand or Mozambique. In females, the ranking is the opposite: Mozambique more than Thailand and Japan.

The female holotype of *Idiosepius macrocheir* has 40 and 44 suckers on each tentacle club. *Idiosepius notoides* have the most suckers on the tentacle club within the genus (♀ 78.72 ± 4.33 and ♂ 62.82 ± 8.53). Notably, *I. notoides* has more injuries on the appendages than any

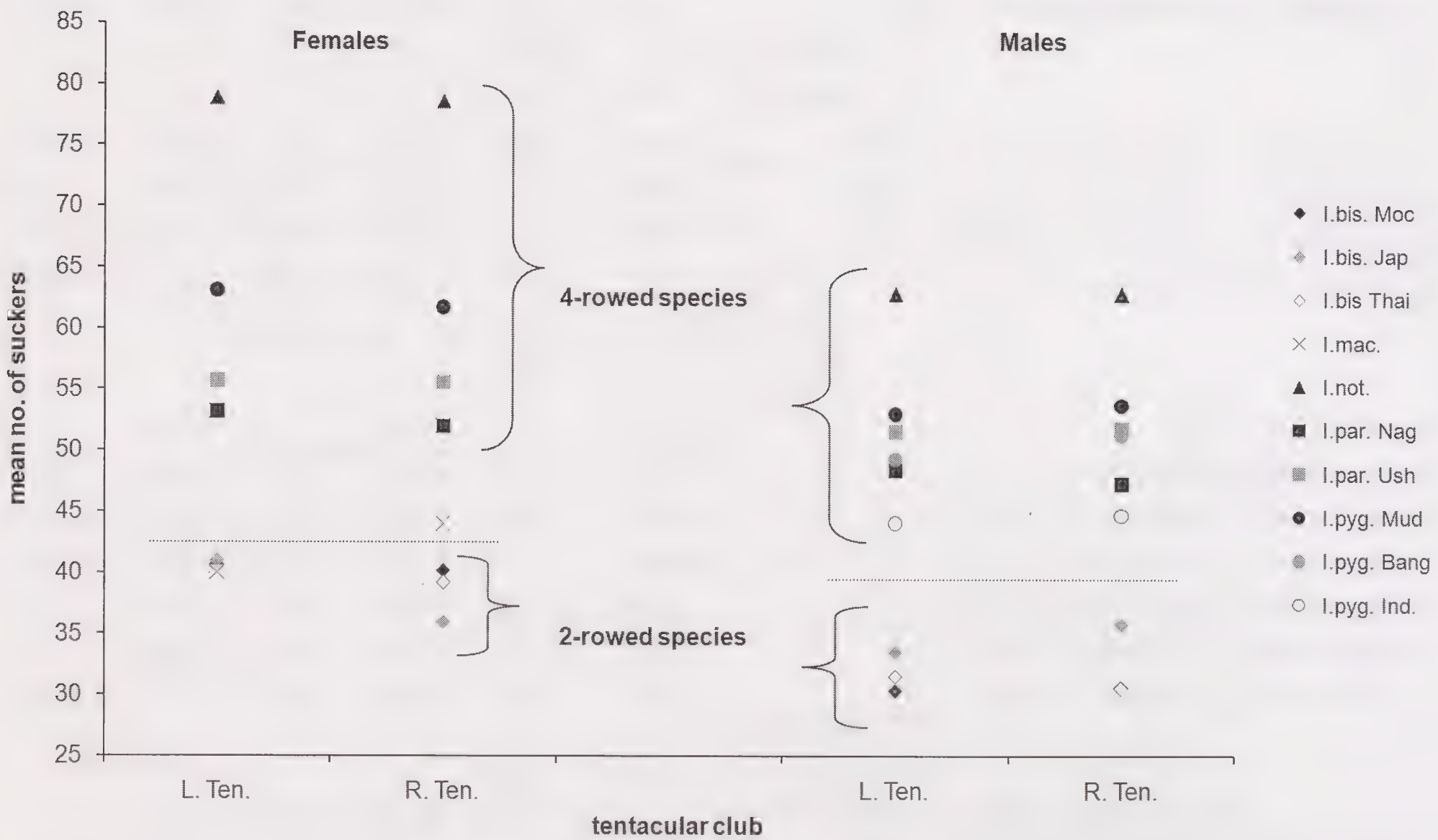


FIG. 3. Average number of suckers on the right (R. Ten.) and left tentacle club (L. Ten.) in females and males in *Idiosepius* spp.

TABLE 4. Number of suckers on appendages in *Idiosepius* spp. (*Data by Chotiyaputta et al., 1991).

Species		No. of suckers on appendages				
		A1	A2	A3	TC	A4
<i>I. biserialis</i> ♀ Moçambique n = 10	mean	23.95	26.75	25.95	40.40	26.70
	S.D.	3.02	1.91	2.42	3.61	3.52
	range	17-29	24-30	20-30	34-46	15-31
<i>I. biserialis</i> ♂ Moçambique n = 10	mean	17.95	21.45	20.30	30.55	4.30
	S.D.	1.61	2.34	2.63	3.44	0.84
	range	15-26	18-28	14-24	24-38	3-7
<i>I. biserialis</i> ♀ Thailand n = 10	mean	21.25	24.30	22.35	39.60	23.45
	S.D.	1.55		2.30	3.49	2.94
	range	19-24	21-28	16-26	34-46	17-28
<i>I. biserialis</i> ♂ Thailand n = 7	mean	14.64	17.72	16.57	31.07	3.79
	S.D.	1.92	0.90	1.27	1.86	0.94
	range	11-18	16-19	15-18	28-34	2-5
<i>I. biserialis</i> ♀ Japan n = 4	mean	16.88	18.50	18.75	38.50	20.00
	S.D.	3.71	2.95	2.99	8.16	1.79
	range	12-23	15-24	15-22	25-48	17-24
<i>I. biserialis</i> ♂ Japan n = 7	mean	17.65	20.07	18.43	34.72	4.15
	S.D.	1.42	2.27	2.02	3.51	0.54
	range	15-20	16-23	14-21	26-38	3-6
Mean (♀)		22.08 ± 2.50			39.50 ± 5.09	
Mean (♂)		18.31 ± 1.82			32.11 ± 2.93	
<i>I. macrocheir</i> ♂ n = 1	total	24+25	27+29	22+30	40+44	29
	mean	30.30	35.27	32.24	78.72	32.50
<i>I. notoides</i> ♀ Snug/Margate n = 8	S.D.	1.53	3.11	2.22	4.33	2.59
	range	27-35	32-40	27-36	70-83	29-38
	mean	26.25	30.97	27.75	62.82	17.31
<i>I. notoides</i> ♂ Snug/Margate n = 18	S.D.	2.82	2.62	3.20	8.53	2.44
	range	22-31	27-34	24-33	48-77	11-26
Mean (♀)		32.60 ± 2.29			78.72 ± 4.33	
Mean (♂)		28.32 ± 2.88			62.82 ± 8.53	
<i>I. paradoxus</i> ♀ Ushimado n = 10	mean	28.10	31.75	29.10	55.65	28.60
	S.D.	2.62	1.69	2.22	3.37	1.95
	range	21-33	28-34	24-32	51-62	25-31
<i>I. paradoxus</i> ♂ Ushimado n = 10	mean	25.50	28.35	26.25	51.70	6.45
	S.D.	2.84	2.73	2.54	6.02	1.06
	range	19-30	24-31	22-30	43-62	4-9
<i>I. paradoxus</i> ♀ Nagoya n = 10	mean	28.85	32.65	29.40	52.60	29.00
	S.D.	2.03	2.00	1.92	3.41	2.37
	range	26-33	29-35	26-33	47-59	24-33

(continues)

(continued)

Species		No. of suckers on appendages				
		A1	A2	A3	TC	A4
<i>I. paradoxus</i> ♂ Nagoya n = 10	mean	25.80	29.30	27.25	47.85	7.15
	S.D.	3.50	3.14	3.51	6.76	1.20
	range	21-33	24-34	22-36	39-63	5-10
	Mean (♀)		29.98 ± 2.08		54.13 ± 3.39	
	Mean (♂)		27.08 ± 3.04		47.98 ± 5.05	
<i>I. pygmaeus</i> ♀ Mudong n = 10	mean	22.80	26.10	26.05	62.40	23.10
	S.D.	2.16	1.87	2.12	3.74	1.97
	range	19-28	21-28	22-30	54-71	20-27
<i>I. pygmaeus</i> ♂ Mudong n = 10	mean	18.65	22.20	21.95	53.35	2.65
	S.D.	1.61	1.99	2.00	2.48	0.80
	range	16-21	19-26	19-25	50-60	1-4
<i>I. pygmaeus</i> ♂ Indonesia n = 10	mean	17.30	20.70	19.75	44.40	2.65
	S.D.	1.59	1.69	1.50	2.37	0.50
	range	12-19	16-23	17-22	41-51	2-3
	Mean (♀)		24.98 ± 2.05		62.40 ± 3.74	
	Mean (♂)		20.09 ± 1.73		48.88 ± 2.43	
<i>I. thailandicus</i> ♀ n = 13*	mean	-	-	-	-	-
	S.D.	-	-	-	-	-
	range	20-24	20-26	18-26	34-45	19-28
<i>I. thailandicus</i> ♂ n = 11*	mean	-	-	-	-	-
	S.D.	-	-	-	-	-
	range	15-16	15-20	15-20	25-35	3-4

other investigated species of *Idiosepius*. Bites on arm pair I and II, on tentacles, and skin injuries on the appendages are frequent in this species; on average, every third animal is affected. Specimens with such injuries on the extremities were excluded from the evaluation.

Individuals of *Idiosepius paradoxus* have 54.13 ± 3.39 (♀) and 47.98 ± 5.05 (♂) suckers; while females from Ushimado have more suckers than those from Nagoya, for males the ranking is the opposite.

Idiosepius pygmaeus has 62.40 ± 3.74 (♀) and 51.84 ± 3.05 (♂) suckers, whereas male specimens from Indonesia have fewer suckers than individuals from Thailand.

Male *Idiosepius thailandicus* have 25–35 suckers on the tentacle club, females 34–45 suckers (Chotiyaputta et al., 1991).

Examining the number of suckers on the tentacle club by species indicates a high significance that may allow a differentiation of the two- and four-row group (Table 5). The significance within the four-row group is small but

provides no species-specific differentiation.

The female paratype of *I. macrocheir* with its 40 and 42 suckers resembles in its number more closely the two-row than the four-row group.

Hectocotylus Shape

In the genus *Idiosepius* both ventral arms in males are hectocotyliized. The following schematic drawings (Fig. 4) provide an overview of the right and left ventral arms according to the literature references. The subsequent SEM images (Fig. 5A–J) give a more detailed picture of its outer shape.

In *Idiosepius biserialis*, both ventral arms are slender, the right ventral arm has two small flaps, separated by a deep cleft, at the tip (Fig. 5A), whereas the left one has a furrow on the aboral side (Fig. 5B). In some males, the hectocotyli arms were somewhat unequal in length; the left arm was shortly shorter than the right one.

Voss (1962) collected and described only a female individual of *Idiosepius macrocheir*; no

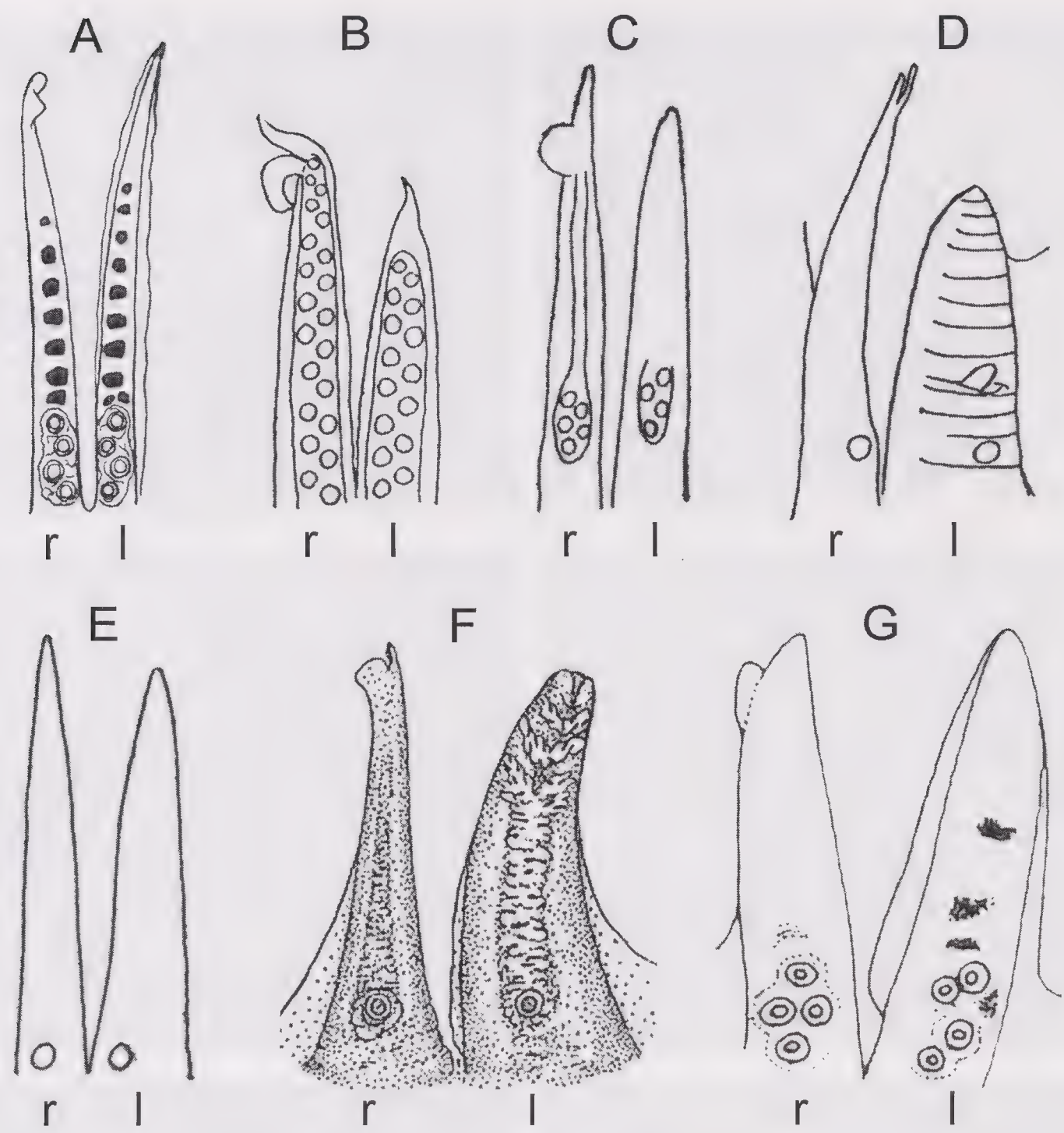


FIG. 4. Schematic drawings of the right (r) and left (l) hectocotylus from the original literature references. (A): Image of *I. biserialis* from Voss (1962); (B): Image of *I. notoides* from Berry (1921a); (C): Image of *I. paradoxus* from Sasaki (1914); (D): Image of *I. picteti* from Joubin (1894); (E): Image of *I. pygmaeus* from Steenstrup (1881); (F): Image of *I. pygmaeus* from Voss (1963); (G): Image of *I. thailandicus* from Chotiyaputta et al. (1991).

TABLE 5. Statistical differences in number of suckers in *Idiosepius* spp.

Species A	Species B	Mean Difference (A–B)	Std. Error	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
<i>I. biserialis</i>	<i>I. notoides</i>	-27.417*	29.751	0.000	-36.168	-18.665
	<i>I. pygmaeus</i>	-16.958*	13.046	0.000	-20.632	-13.284
	<i>I. paradoxus</i>	-17.858*	15.411	0.000	-22.239	-13.478
<i>I. notoides</i>	<i>I. biserialis</i>	27.417*	29.751	0.000	18.665	36.168
	<i>I. pygmaeus</i>	10.458*	31.245	0.017	1.438	19.478
	<i>I. paradoxus</i>	9.558*	32.304	0.040	0.323	18.794
<i>I. pygmaeus</i>	<i>I. biserialis</i>	16.958*	13.046	0.000	13.284	20.632
	<i>I. notoides</i>	-10.458*	31.245	0.017	-19.478	-1.438
	<i>I. paradoxus</i>	-0.900	18.127	0.997	-5.942	4.142
<i>I. paradoxus</i>	<i>I. biserialis</i>	17.858*	15.411	0.000	13.478	22.239
	<i>I. notoides</i>	-9.558*	32.304	0.040	-18.794	-0.323
	<i>I. pygmaeus</i>	0.900	18.127	0.997	-4.142	5.942

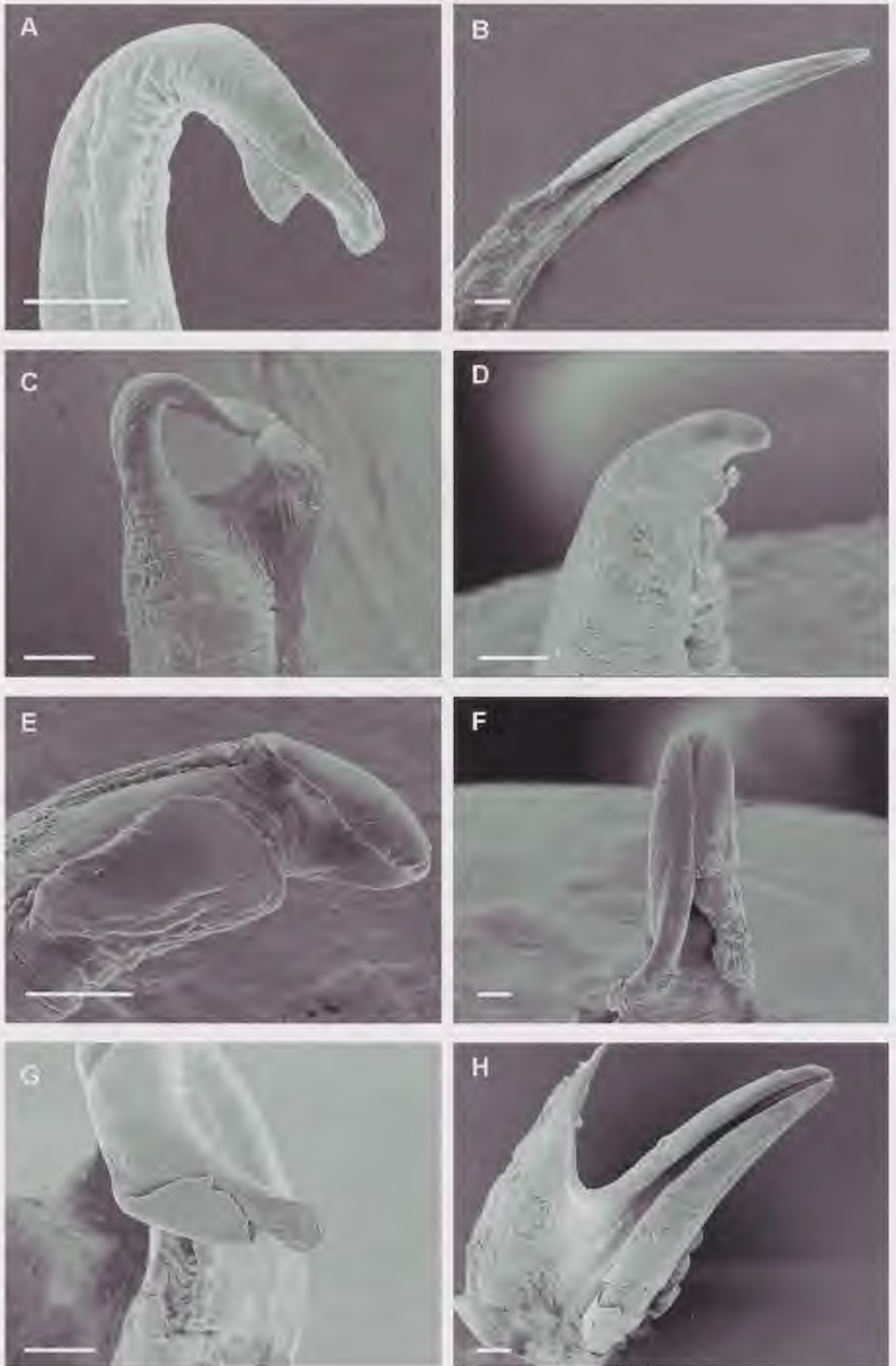


FIG. 5. SEM images of the hectocotyli of male *Idiosepius* spp. (A): Right ventral arm of *I. biserialis*; (B): Left ventral arm of *I. biserialis*; (C): Right ventral arm of *I. notoides*; (D): Left ventral arm of *I. notoides*; (E): Right ventral arm of *I. paradoxus*; (F): Left ventral arm of *I. paradoxus*; (G): Right ventral arm of *I. pygmaeus*; (H): Left ventral arm of *I. pygmaeus*. Scale bar = 200 μ m.

TABLE 6. Inter- and intraspecific variation in sucker number on both ventral arms in *Idiosepius* spp. (#Data by Joubin, 1894; *Data by Chotiyaputta et al., 1991).

Left/right ventral arm	<i>I. biserialis</i>				<i>I. notoides</i>	<i>I. paradoxus.</i>	<i>I. picteti</i> #	<i>I. pygmaeus</i>	<i>I. thailandicus*</i>	
	Moç.	Jap.	Ind.	Thail.				Thail.	Ind.	
	N = 52	N = 7	N = 1	N = 7	N = 20	N = 116	N = 1	N = 64	N = 40	N = 11
0/0								1		
1/1							1	2	1	
1/3	2							1		
1/4	1									
2/1	1									
2/2				1				5	6	
2/3	2							21	11	
2/4	1					1		1		
2/5	3									
3/2									4	
3/3	4							24	13	
3/4	6	1		2				7	4	11
3/5	12	4		1						
3/6	1									
3/7	1									
4/3	2							1		
4/4			1					1	1	
4/5	11	1		3		3				
4/6	1	1				3				
4/7						2				
4/8	1					1				
5/5	2					3				
5/6						12				
5/7						13				
5/8	1					7				
6/5						1				
6/6						7				
6/7						12				
6/8						16				
6/9						2				
6/10						2				
7/6						2				
7/7						5				
7/8						8				
7/9						8				
7/10						2				
8/9						2				
8/10						1				

(continues)

(continued)

	<i>I. biserialis</i>				<i>I. notoides</i>	<i>I. paradoxus.</i>	<i>I. picteti</i> #	<i>I. pygmaeus</i>	<i>I. thailandicus*</i>
Left/right	Moç.	Jap.	Ind.	Thail.				Thail.	Ind.
ventral arm	N = 52	N = 7	N = 1	N = 7	N = 20	N = 116	N = 1	N = 64	N = 40
									N = 11
8/11						1			
9/9						1			
9/12						1			
11/15					1				
11/19					1				
12/16					1				
12/17					1				
13/18					1				
13/19					2				
13/22					3				
14/19					1				
14/21					1				
15/19					1				
15/21					1				
15/23					2				
15/26					1				
16/25					1				
17/27					1				
18/20					1				

information about the modified ventral arms in males is available.

The right ventral arm of *Idiosepius notoides* is slightly longer than the left, with a few more suckers and with a double flap on its tip (Fig. 5C). The left ventral arm is small and broad, its tips singular end narrow and pointed without any appendages (Fig. 5D).

In *Idiosepius paradoxus* both ventral arms have the same length. The right one has a semicircular membrane on the dorsal side near the tip. The tip itself ends as a broad “cap-like” cover (Fig. 5E, F). The left ventral arm has fleshy ridges on the oral side and, as *I. biserialis*, a furrow on the aboral side (Fig. 5G), which was not mentioned in the original description and drawing.

According to Joubin (1894), the right ventral arm of *Idiosepius picteti* is slender, long and bilobated at the tip. He also reported that the left ventral arm in male *I. picteti* is very short and broad (Fig. 4D).

The description and morphology of the hectocotylus of *Idiosepius pygmaeus* corre-

sponds more to the schematic drawing of Voss (1963) (Fig. 4F) than to those of Steenstrup (1881) (Fig. 4E). As in *I. paradoxus*, also in *I. pygmaeus* both ventral arms have the same length. The right arm in *I. pygmaeus* is thinner and slender but two-lobed at its tip (Fig. 5H). The left ventral arm is stout and thick and has fleshy ridges on the oral and a furrow on the aboral side (Fig. 5I).

According to Chotiyaputta et al. (1991) (Fig. 4G), the right arm of *Idiosepius thailandicus* is much thicker and has a small membrane at its tip, while the left hectocotylized arm is slender with a distinct lateral membrane.

In some species – *I. biserialis* *I. paradoxus*, *I. pygmaeus*, *I. thailandicus* – the left ventral arm is furrow-like aborally, a feature absent in *I. notoides* and *I. picteti*. The right arm mostly carries appendages, such as membranes, or is modified at its tip. Although this characterization mostly corresponds to the description in the original literature, some aspects (description of *I. paradoxus*) are added. In summary, the shape of the fourth arm pair as well as

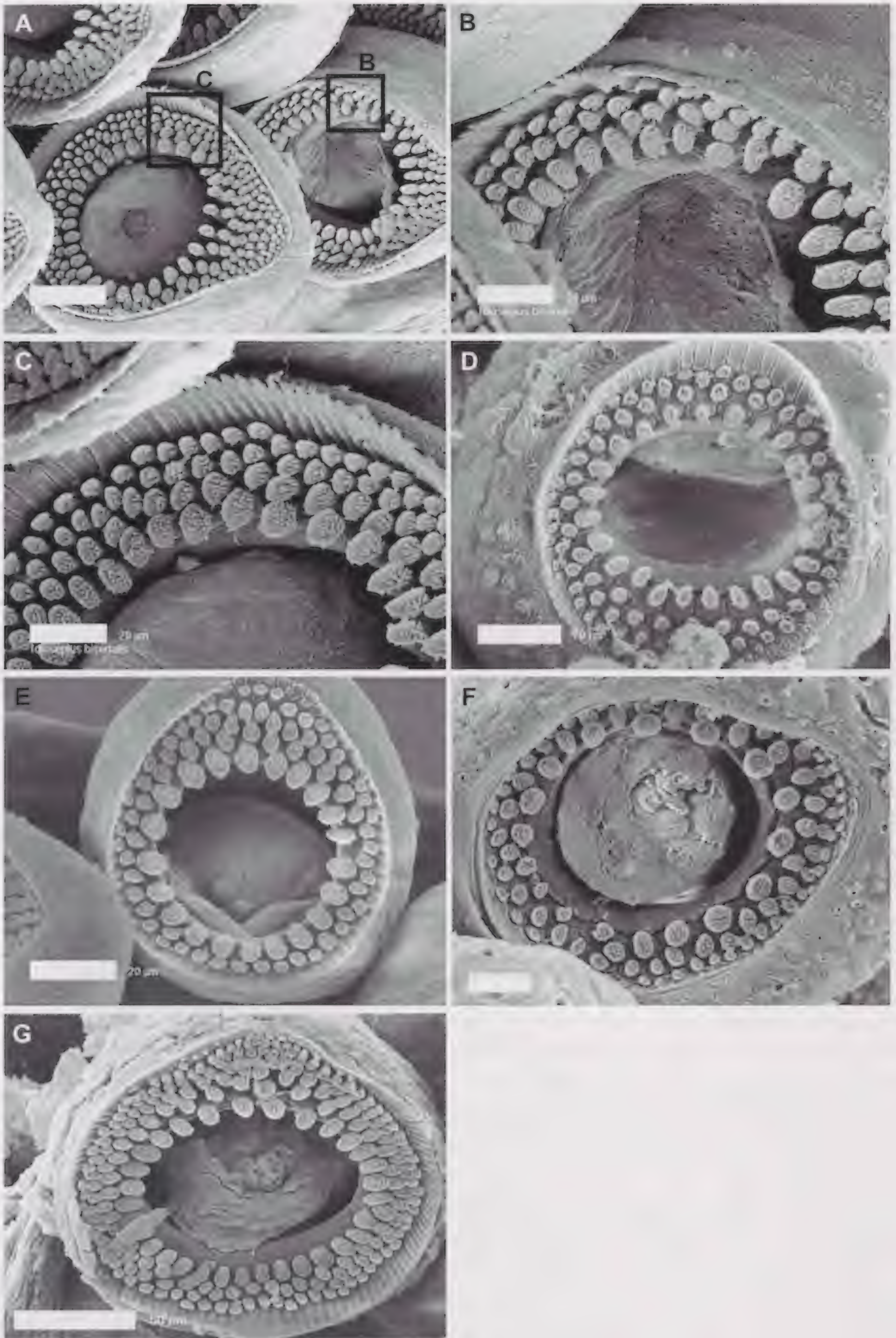


FIG. 6. Suckers on tentacle of *Idiosepius* spp. (A–C): *I. biserialis* (Mozambique) with a 3- (B) and 4-series (C) arrangement of pegs; (D, E): In some cases a 2- to 3-series arrangement of pegs on arm (D) or tentacle sucker (E) is present; (F, G): Suckers on arm (F) and tentacle (G) of *I. thailandicus* paratype show a 3-series arrangement of pegs. Scale bar = 50 μm (A, G); scale bar = 20 μm (B–F).

its appendices varies between the species and therefore provides a strong feature for its characterization.

Suckers on Hectocotylus

All investigated specimens are believed to have fully developed hectocotyli, except for certain individuals of *I. notoides* with partly malformed ventral arms. Strong inter- and intraspecific variation in sucker number was found on both ventral arms (Table 6): *Idiosepius biserialis* from Mozambique have 1–5 suckers on the left and 3–8 suckers on the right ventral arm. Predominant are the combinations 3/4, 3/5 and 4/5 suckers on the left/right ventral arms, but variations from 1/3 to 4/8, 5/5 and 5/8 are present. In the specimens from Thailand, 3/4 and 4/5 suckers on left/right ventral arms are also common. The individual from Indonesia has four suckers on each arm, whereas specimens from Japan mainly have three suckers on the left and five on the right ventral arm.

Idiosepius notoides has the highest number of suckers on the hectocotylized arms (11/15 to 18/20 suckers), whereas the combinations 13/19, 13/22, and 15/23 suckers are somewhat more common.

Idiosepius paradoxus exhibit the greatest variability in sucker combinations: 4–9 suckers on the left and 5–12 suckers on the right ventral arm. The combinations 5/6, 5/7, 6/7 or 6/8 suckers are most frequent. One individual has 2/4 suckers.

The male holotype of *Idiosepius picteti* has only one sucker on each ventral arm (Joubin, 1894).

Idiosepius pygmaeus (Mudong) sucker combinations vary from 0–4 suckers on the hectocotylized arms. More than 30% of the specimen have 2/3 suckers on the left/right or three suckers on both ventral arms. Specimens from Indonesia predominantly have two or three suckers on the left and three suckers on the right ventral arm; one individual has 1/1, another 4/4 suckers.

According to Chotiyaputta et al. (1991), male *Idiosepius thailandicus* have 3–4 suckers on the basal area of the hectocotylus. Variations in this species have not yet been described.

Within the two-row group, similar variations of sucker number are present and enable no clear distinction between *I. biserialis* and *I. thailandicus*. Due to the limited overlap in ranges of sucker numbers, the species (*I. notoides*, *I. paradoxus* and *I. pygmaeus*) of

the four-row group are well defined. A single sucker on the hectocotyli is present in *I. picteti*, *I. pygmaeus* from Thailand and *I. pygmaeus* from Indonesia.

Sucker Ultrastructure

All species of *Idiosepius* including the re-examined paratype of *I. thailandicus* (Fig. 6F, G) have suckers with mostly three or four rows of pegs in the suckers of the tentacles and arms. Two rows are also present in the suckers, although this is not only restricted to *I. thailandicus* but present in all *Idiosepius* species. Sometimes this variation arises on the same appendage (Fig. 6A–C) or even on a single sucker (Fig. 6D, E).

Not only in the paratype of *I. macrocheir*, as proposed by Voss, 1962, but also in *I. biserialis* and *I. thailandicus* the suckers in the middle

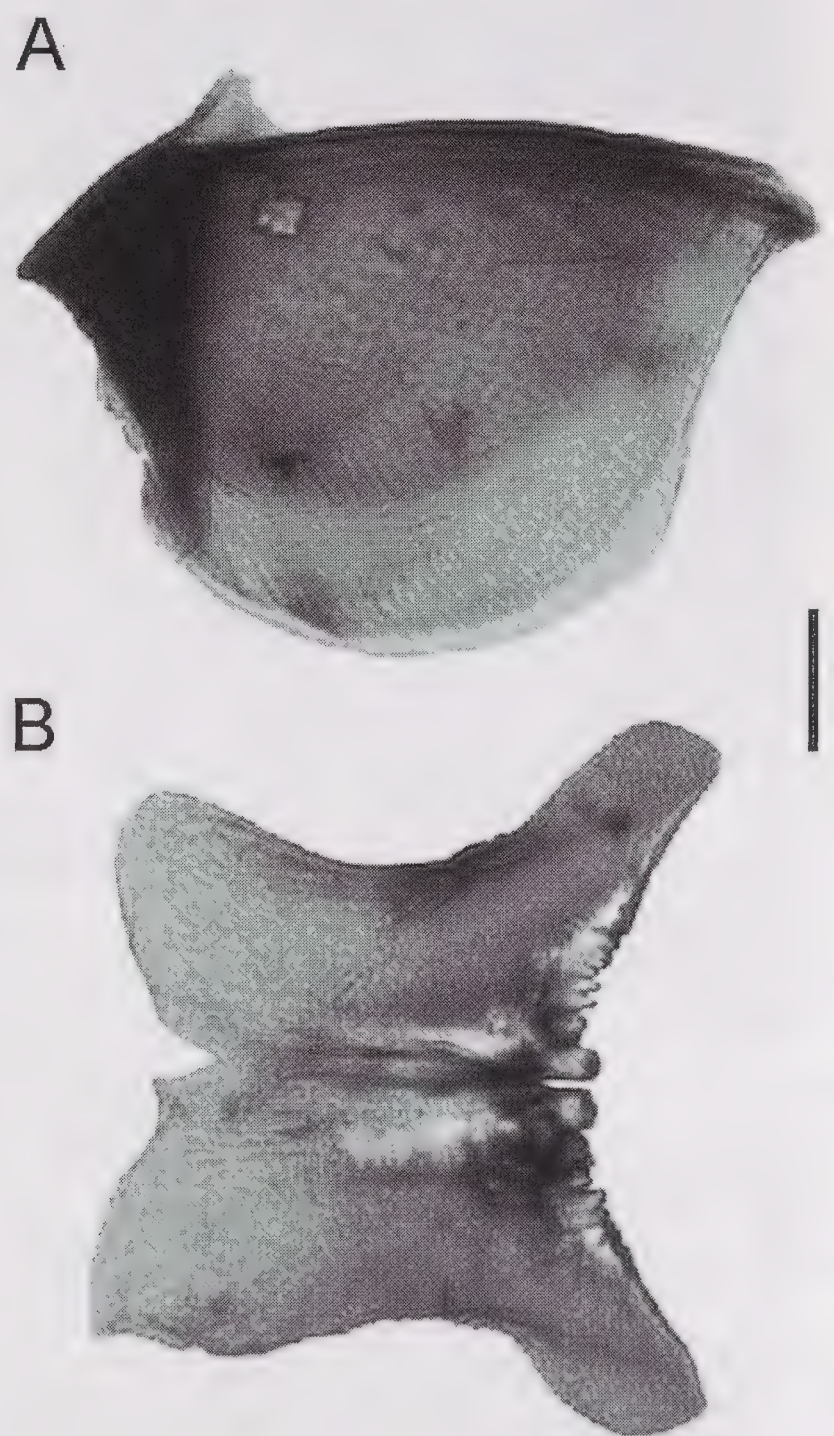


FIG. 7. Beaks of *Idiosepius* spp. (A): Side view of the upper beak from male specimen of *I. pygmaeus* (Bangrong); (B): Top view of the lower beak of male specimen of *I. paradoxus* (Nagoya). Scale bar = 252 μm (A); scale bar = 248 μm (B).

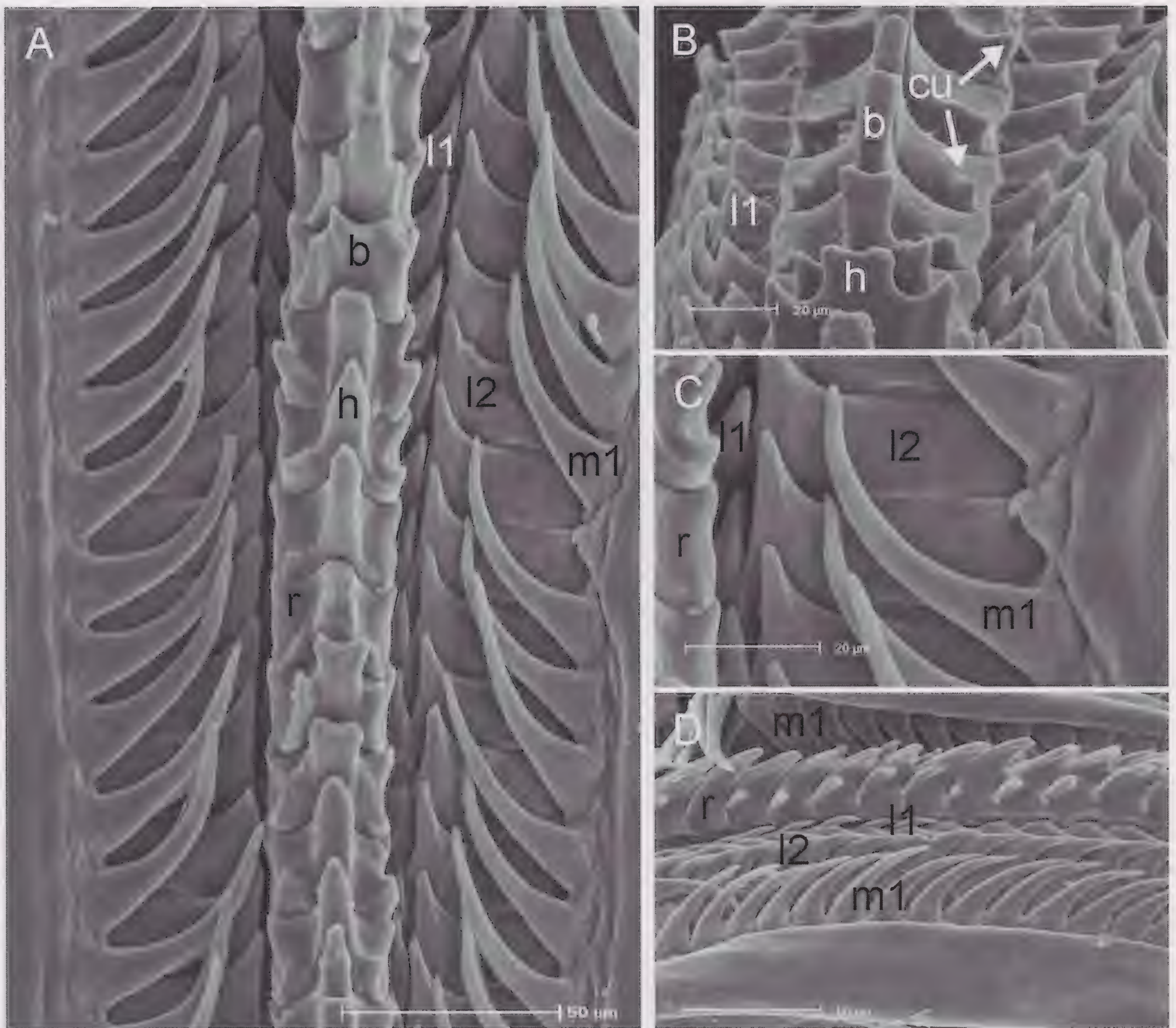


FIG. 8. Radula of *Idiosepius* spp. (A–C): Rhachidian teeth ((r) tall and homodont (h), compact and bidentate (b), cones and cusps (cu), two lateral teeth (l1 and l2) and the marginal tooth (m1)); (D): Radula seen from the right.

part of tentacle club are larger (about 1/4) than those at its base and tip, while in arms only the suckers at the tip are smaller. This attribute is lacking in the four-row species *I. notoides*, *I. paradoxus* and *I. pygmaeus*.

In all species, around every 20th individual of both sexes has only half-sized suckers in the middle part of the tentacle club (Fig. 10B). Since sucker pedicels were also frequently found during sucker evaluation, these are probably regenerated suckers.

Peg arrangement or sucker structure does not differ between the sexes and/or species. Our investigations show that the sucker form (and therefore its peg arrangement) is strongly influenced by fixatives, abnormal growth, and contraction of the arms and tentacles.

Beaks

The beaks in all species have a serrated cutting edge, apparent in both upper and lower beak (Fig. 7). The upper and lower beak has a black horny hood, whereas the lateral walls are colorless. Additionally, the upper mandible has a smooth inner rostrum, a short hood, which is low on the crest, and widely spread lateral walls, which have a shallow indentation of the posterior wall margin.

Although the two-row species *I. biserialis* from Mozambique and Thailand (*I. biserialis* from Japan and Indonesia were not evaluated) and *I. thailandicus* have smaller lower beaks than the four-row species, the evaluation provides no discernable differences of the upper beaks of any *Idiosepius* species.

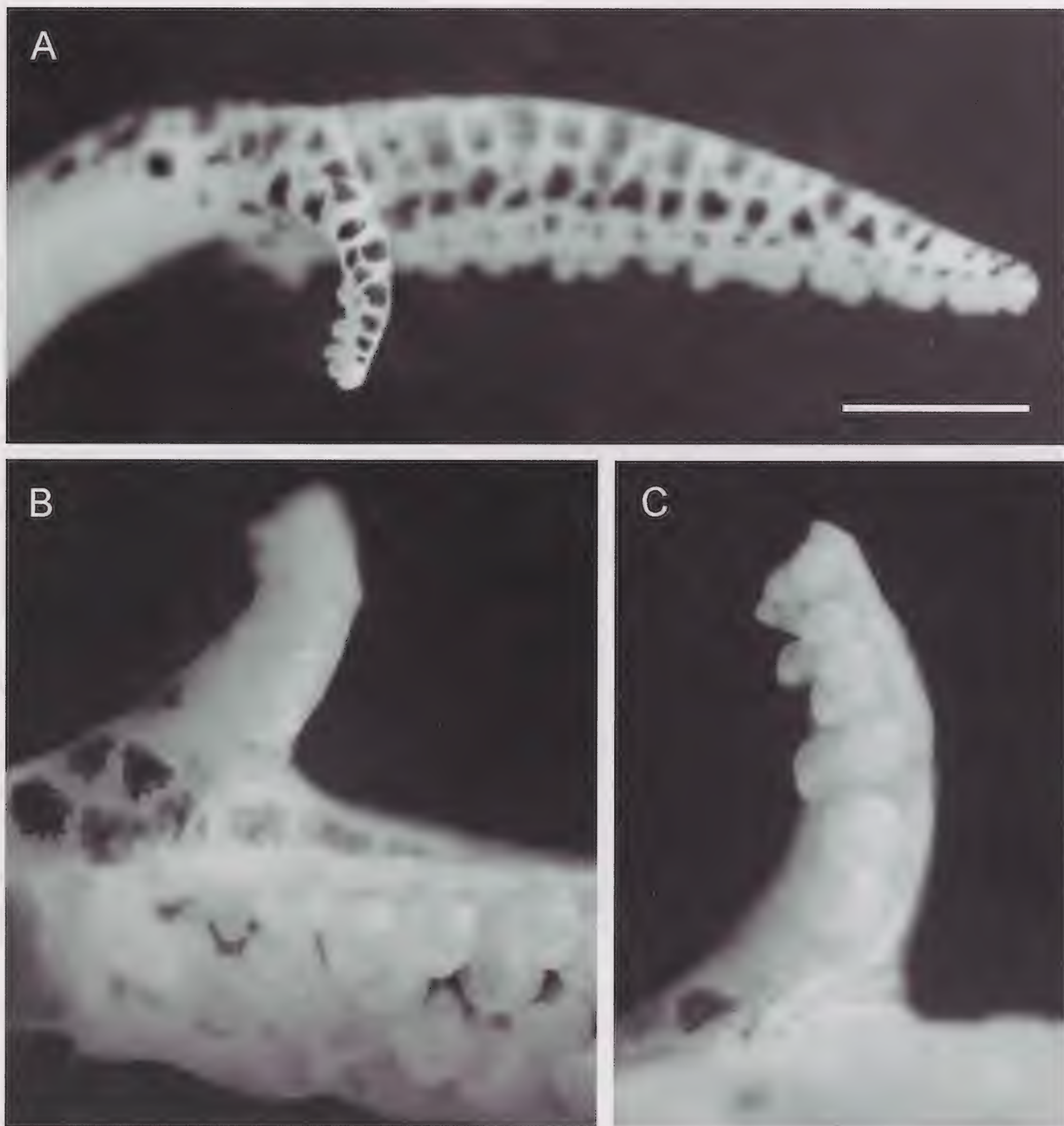


FIG. 9. Right tentacle of female *Idiosepius paradoxus*. (A): Overview; (B): Extra 'arm-like' structure; (C): Suckers. Scale bar = 1 mm.

Radula

The nomenclature of Nixon (1985) has been used in the following discussion. In all examined *Idiosepius* species ($n = 5$ of each species and location, except *I. biserialis* from Japan and Indonesia; *I. macrocheir* and *I. picteti* were not investigated), seven elements are present in the radula: the rhachidian tooth (*r*) is large. On either side of the rhachidian tooth, a first and

second lateral tooth (*l1* and *l2*) are present. Next to these, the marginal teeth (*m1*) complete the seven elements (Fig. 8A–D). Other elements such as a marginal plate are missing in this genus.

The rhachidian tooth exhibits a median cone with a series of tall homodont (*h*) or compact bidentate (*b*) cones. Cusps (*cu*) beside the cone are present in both types but they are more prominent in the bidentate type.

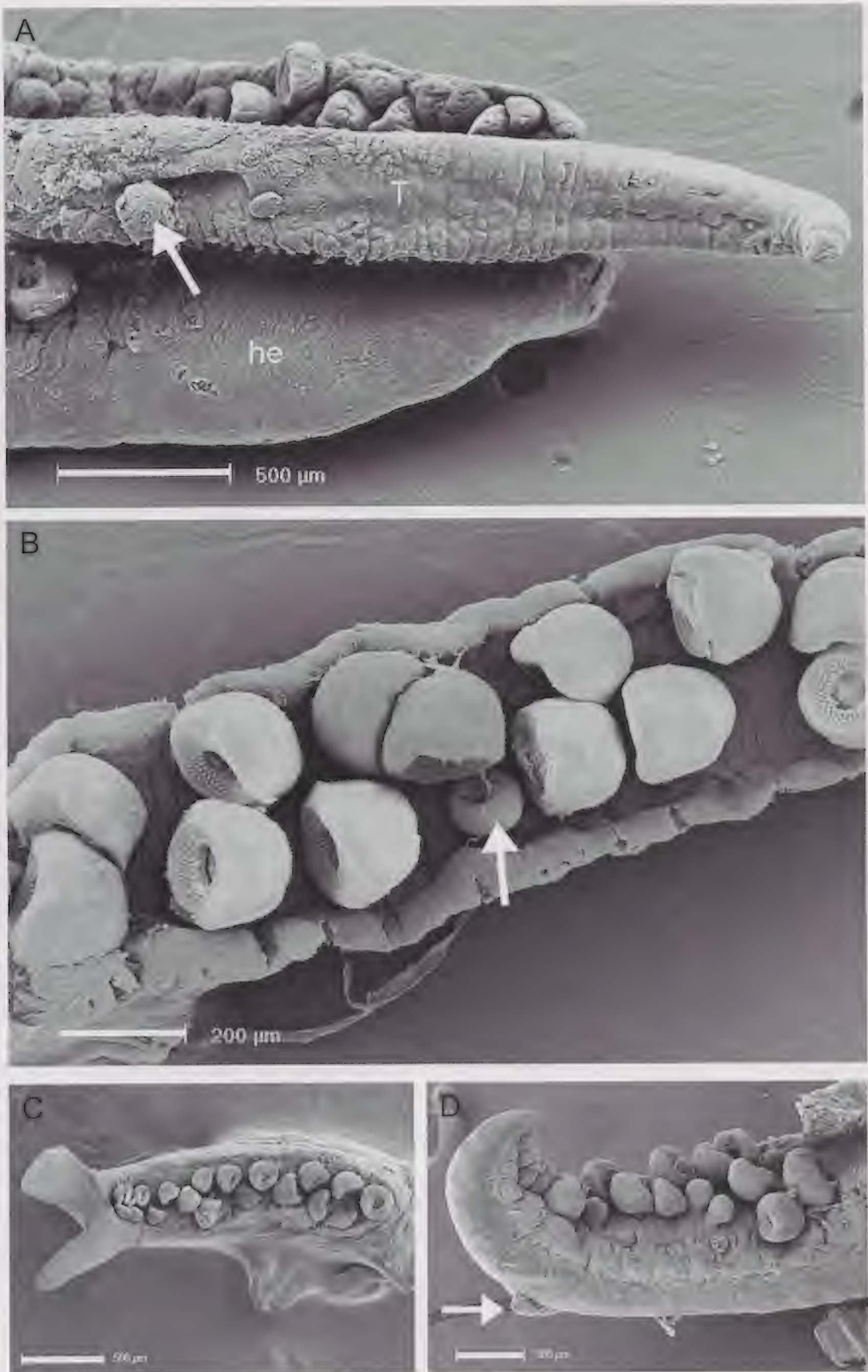


FIG. 10. Tentacles of *Idiosepius* spp. (A, B): Male *I. paradoxus* (A) with only one sucker (arrow) on the right tentacle (T) and adjacent hectocotylus (he). Residual structures like sucker shafts are absent (B). Tentacle with half-sized suckers are indicated by arrows; (C, D): In *I. notoides*, deformations in the right hectocotyli are visible. While the normal ventral arm has two small flaps (C), in some hectocotyli these appendages (arrow) are reduced or missing (D). Scale bar = 500 μm (A, C); scale bar = 200 μm (B, D).

The two lateral teeth are unicuspid but vary in shape and size. The tooth I1 is small, somewhat triangular and increases in height along of the ribbon. The lateral tooth I2 has longer cusps and is laterally ridged. The marginal tooth is sabre-shaped and the tallest element in the radula.

Within species, no differences were observed between the sexes in the arrangement or structure of the radula. Size differences of the teeth correlate with mantle length of the animals. Only the radula of *I. notoides* is distinct from the other species in the absence of bidentate cones on the rhachidian tooth.

Malformations

Apart from the fixation-induced body and/or tentacle deformation, abnormal growth was found in the tentacles and their suckers in *I. paradoxus* (Nürnberg et al., 2006). In one female, an extra “arm-like” structure branched basally from the right tentacle (Fig. 9A–C). This appendix was smaller than the tentacle, with suckers arranged irregularly or in pairs. One male developed only one sucker on the right and no suckers on the left tentacle. Even residual structures such as sucker stalks or injuries were not visible (Fig. 10A).

Malformation of the hectocotylus was recorded only in *I. notoides* specimens. While the normal right ventral arm has two flags at its tip (Fig. 10C), in many individuals (about 11 of 20 investigated specimens) the flaps were less strongly developed or missing (Fig. 10D).

DISCUSSION

Since the discovery of *I. thailandicus* by Chotiyaputta et al. (1991), questions have been raised about the taxonomic characters proposed by Nesis (1982). The aim of this study is to re-evaluate several morphological attributes in all nominal *Idiosepius* species and find reliable diagnostic characters that are valid for all.

The present study indicates that such highly plastic characters as mantle length, the counts and arrangement of suckers on the tentacle club, and other potential features (body shape, cornea fixability or contour of the adhesive organ) (Boletzky et al., 2005), fail to discriminate the species of *Idiosepius*. Handling and fixation strongly influence these characters, leading to misinterpretations for *Idiosepius* (Byern & Klepal, 2007) as well as for other cephalopod

groups (Allcock et al., 2008; O’Shea, 1997; Voight, 2001).

Even though the sucker arrangement on the extremities and its arrangement provides a reliable trait on taxa level for octopodids (Toll, 1988; Voight, 1993), a grouping of the *Idiosepius* species (two- and four-row), as done by Nesis (1982), seems to be less appropriate in view of induced sucker missarrangements and should therefore be rejected.

Also, the characterization of the *Idiosepius* species by sucker counts on the hectocotylus is of doubtful use. Earlier studies by Appellöf (1898), Sasaki (1914), and Hylleberg & Nateewathana (1991b), as well as the present study, pointed out that its number vary strongly leading to overlaps between some species (i.e., *I. biserialis* and *I. pygmaeus* or *I. picteti* and *I. pygmaeus*).

Of all here evaluated morphological attributes, only the shape of the ventral arms with its appendages (e.g., double flag, cup-like tip, etc.) allows a clear and reliable classification of the *Idiosepius* species. However, we are aware that this taxonomic classification is only applicable for males; female individuals, as in particular given for *I. macrocheir*, still remain indistinguishable based on this attribute.

The homodont rhachidian tooth should be used as an additional character to distinguish at least the females of *I. notoides* from the remaining species; nonetheless, we are still unable to find other morphological characteristics that would allow a unisex species classification.

Aside, the present study indicate that the characterization of *I. thailandicus* and *I. macrocheir* by the morphological criteria proposed by Chotiyaputta et al. (1991) and Voss (1962) are of doubtful use.

Idiosepius thailandicus provide no systematic relevant differences to *I. biserialis* either in hectocotylus shape and appendages, sucker size dimorphism, and peg arrangement on the tentacle clubs as well as other evaluated morphological attributes.

Due to the simultaneous and independent discovery of *I. thailandicus* (Chotiyaputta et al., 1991) and *I. biserialis* (Hylleberg & Nateewathana, 1991a) in Thailand, we suggest that the authors may have described the same species; thus, *I. thailandicus* was wrongly characterized as single species however rather represents individuals of *I. biserialis*.

This hypothesis is supported by cross-mating experiments (Nabhitabhata et al., 2006; Nabhitabhata & Suwanmala, 2008), in which individuals of *I. biserialis* and *I. thailandicus* mate

with each other, producing fertilized eggs from which embryos hatched. However, since cultivation of *Idiosepius* hatchlings in aquaria is still limited (Byern et al., 2006), it was not possible yet to verify the fertility of these *I. biserialis*-*I. thailandicus* hatchlings.

It also remains questionable whether both taxa are able to come together in nature. Since our knowledge about the genus *Idiosepius* is still marginal, relatively little is known about the biology, life cycle or geographical distribution of the species. Observations (Suwanmala et al., 2006; Byern & Klepal, 2007) indicate that *I. biserialis* and *I. pygmaeus* partly occur in neighbored areas, whether this is also valid for *I. biserialis* and *I. thailandicus* or other species remains unclear up to now.

Based on the sucker arrangement, the female holotype *I. macrocheir* belongs to the four-row group, as stated by Voss (1962). However, the sucker size dimorphism, sucker disarrangement as well as sucker number on the tentacle clubs place this species more towards the two-row species *I. biserialis*.

Based on our results, we suppose that *I. macrocheir* was likewise wrongly assigned as single species but rather represents an individual of *I. biserialis*. However, since the holotype of *I. macrocheir* is a female, a detailed characterization by the shape of the hectocotylized arms and their appendages, as given for the other *Idiosepius* species, is lacking in this case.

Additionally, several collection expeditions by the South African Museum in this region have been undertaken since Voss (1962). None yielded further individuals of *I. macrocheir* that would verify the presence of four-row individuals in African waters.

This study is a first attempt to compare all species of the genus *Idiosepius* and provide new insights into its relationships. Nevertheless, additional collections and evaluations as well as practical verification of the proposed systematic characterization based on the hectocotylus by other researchers are necessary to provide a more complete picture of the genus *Idiosepius* and, ultimately, to help re-organize its systematic key.

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USING DISPERSAL RATES TO GUIDE TRANSLOCATION ACROSS IMPERMEABLE WILDLIFE RESERVE BOUNDARIES: HAWAIIAN TREE SNAILS AS A PRACTICAL EXAMPLE

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ABSTRACT

Discontinuous wildlife reserves can lead to inbreeding depression for fragmented populations of threatened species. To offset such effects, conservation managers frequently turn to translocation strategies, such as the one-migrant-per-generation rule (OMPG), which relies on many unrealistic assumptions of Wright's (1931) island model. We therefore propose an alternate translocation approach based on the natural dispersal rates of focal species, using two endangered Hawaiian tree snails species, *Achatinella sowerbyana* and *A. mustelina*, as practical examples. The rate at which tree snails historically dispersed across reserve boundaries can be used to guide contemporary translocation across those dispersal barriers. Snail movements were monitored for three years using capture-mark-recapture (CMR) methods, and analyzed with a multi-strata model in program MARK to obtain survival and dispersal rates. We tested and ranked models, including age, time, weather, and location effects on survival, dispersal, and capture probabilities. Annual mortality ranged from over 50% to less than 20%, by site, mirroring expectations from anecdotal observations of predator abundances. Monthly dispersal rates between isolated tree clusters were recorded between 3% and 24% of a population, depending on the population's exposure to severe weather rather than its species designation. Simulations based on dispersal-distance distributions were then applied to estimate emigration rates beyond the finite study sites. Emigration rates ranged among sites from 0.7% to 6.7% of the population per month, translating to between 6 and > 100 emigrants per year, depending on the density of snails at each site and the site's dimensions. The site boundaries are directly analogous to current and future reserve designs, and we show how such emigration rates can be used to guide two-way translocation rates across such artificial barriers.

Key words: *Achatinella*, OMPG, Program MARK, CMR, conservation.

INTRODUCTION

Across the globe, habitat loss and other anthropogenic causes have led to a drastic decline in biodiversity over the past century (IUCN, 2009). Many formerly vast and continuous ranges of animal species have been reduced to patches of fragmented habitat. The most common and intuitive conservation approach involves protecting the survivors' remnant natural habitat through reserve designations. Often, however, these reserve systems comprise only a fragmented landscape of former species distributions, with no means of natural connectivity among them.

All but the most vagile of species are restricted to mating only with other individuals within such isolated reserves. While not especially problematic in large populations, individuals in smaller threatened populations are forced to mate with relatively closer relatives by default, or might even avoid mating entirely (Ingvarsson, 2002). For species that normally outbreed with distinctly non-related members of the population, this can have dire consequences. Inbreeding depression, the reduced fitness resulting from breeding of closely related individuals, is a major concern when managing the survival of any small and threatened population (Leberg, 1990).

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To mitigate mating avoidance and inbreeding depression effects, as well as to prevent artificial divergence among fragmented subpopulations, conservation managers often advocate the reestablishment of migration corridors (Beier & Noss, 1998). However, logistical constraints, such as urbanization (e.g., roads forming barriers and land use changes), often preclude the feasibility of establishing such corridors for many species. Those species are then prime candidates for translocation. This strategy involves the human-assisted movement of individuals between reserves to restore some level of historical and natural connectivity.

The one-migrant-per-generation (OMPG) rule (Mills & Allendorf, 1996) is still the most common guideline for translocations in conservation management. However, OMPG is based on many unrealistic assumptions, such as Wright's (1931) island model, which assumes that natural migration is equally likely between any pair of populations regardless of the distance between them. This suggests that each migration event provides recipient populations with a random genetic sample of the entire species.

Few species actually fit this pattern, because migration between nearest neighbor populations is much more common for most species. A migrant from a closely related neighbor population would thus have a substantially lower effect at overall species homogenization than would a distantly related migrant from across the species' range (Mills & Allendorf, 1996). In light of this, more migrants than OMPG may be necessary from local neighbor populations if one is to mimic natural migration, prevent the divergence of populations, and reduce inbreeding concerns (Mills & Allendorf, 1996).

We discuss only translocation among neighboring populations in this paper, because the consequences of excessive outbreeding from distantly related populations could be equally detrimental to species survival (Edmands, 2007). To employ some modification of OMPG using neighbor populations, one would first need to address a difficult question: how many migrants from neighboring geographic sources would provide the equivalent amount of new alleles to an inbred population, as would a single random migrant sampled from the entire species? We instead suggest an alternative translocation approach that mimics the historical levels of gene flow that a migration corridor would have provided. If the natural migration

patterns of a species can be approximated, it may be possible to artificially mimic historical connectivity among now-fragmented populations.

The entire pulmonate genus *Achatinella*, endemic to the island of O'ahu, Hawai'i, is listed as "critically endangered" (IUCN, 2009). Several remnant species exist as recently fragmented populations in need of translocation. We use these snails to demonstrate a real-world practical application of our approach. The main contemporary threat to these species' survival is from invasive predators, and efforts to create protected snail reserves are already underway (Hadfield et al., 2004). Two *Achatinella* spp. populations have already received predator-proof enclosure fences for *in situ* preservation, with more planned in the coming years.

However, the impermeable nature of these enclosures leaves open the possibility of excessive inbreeding that could ultimately reverse any progress towards protecting these snails. Without a translocation strategy, confining snails to enclosures further restricts gene flow among these already severely fragmented populations. However, if following the erection of a fence there are still individuals in the vicinity of the fenced-off area, then localized translocation is still possible.

Preliminary studies have revealed that these strictly arboreal snails disperse primarily by being blown off of trees by strong wind gusts, then climbing up the nearest vegetation (Hall & Hadfield, 2009). We investigated the rate at which this migration occurs by monitoring two *Achatinella* spp. using capture-mark-recapture (CMR) techniques. Although assessing dispersal rates was our primary objective, our analyses also accounted for variation in recapture and survival probabilities to reduce bias in our estimated dispersal rates. Resultant survival rates could further be used to assess the immediacy of threats to populations, and to prioritize conservation initiatives.

Achatinella mustelina Mighels, 1845, and *A. sowerbyana* Pfeiffer, 1855, were selected for this study because they are both relatively abundant and represent opposite extremes of the genus with regards to climate (Hall & Hadfield, 2009) and evolutionary history (Holland & Hadfield, 2004). It was thus hoped that any resulting similarities might be applicable to conservation efforts for all species in this genus. Our data provided a basis for estimating emigration across potential reserve boundaries, and for guiding rates of future translocation.

METHODS

Data Collection

Two replicate sites were selected for each species and are located at the extreme north/south ends of the known species ranges to further account for any climatic variation (Fig. 1). These are Palikea (Nature Conservancy Hono'uli'uli Preserve) and Kahanahāiki (Makua Military Reservation) in the Wai'anae Mountains for *A. mustelina* (18 km apart), and north of the Poamoho monument (Ko'olau Summit Trail (KST)) and west of 'Ōpae'ula Cabin (Army leased land, west of the KST) in the Ko'olau Mountains for *A. sowerbyana* (2 km apart). A grid of quadrats, each 2.5 m x 2.5 m, was laid out covering the entire area within a site's boundaries (each site enclosing < 1,500 m²). The number of quadrats varied substantially among sites due to local terrain; steep cliffs were present in some sites that were unsafe to survey (Fig. 2).

Surveys to monitor snail dispersal were conducted at each site from late 2005 (month varied by site) to August 2008. Intervals between surveys were roughly three months, although with some variability. In total, nine surveys were completed at 'Ōpae'ula, ten at both Palikea and Poamoho, and 12 at Kahanahāiki. Surveys were conducted on single-day trips by two observers, and 3–5 minutes were devoted to each quadrat (more time was devoted to quadrats with higher density vegetation). A final survey at each site was conducted over the course of two

days in August 2008, involving four observers to maximize long-term dispersal detection. This increase in snail sighting probability for the final survey was accounted for in the analyses.

All surveys involved recording location data of recaptured snails and marking new ones. Dispersal was measured as the distance between the centers of trees, with "trees" also referring to clusters of trees with overlapping branches (rarely > 5 m² at any site). Snails can freely disperse between such connected trees, and our focus was on the wind-dispersed movements between unconnected trees.

Capture-Mark-Recapture

Every snail found was measured (shell length and width) and labeled with a unique code upon first capture. Snails with shells over 7 mm in length were alpha-numerically marked using letters and numbers printed on paper punch-outs (one for the letter and one for the number). Six-point font characters were printed onto waterproof paper (Rite-In-The-Rain), and cut out with a leather punch. In the field, the snail's shell was gently dried and cleaned, and then a small drop of cyanoacrylic glue (Satellite City "Super T") was applied to it. The two punch-outs were then placed onto the glue, followed by another drop of the transparent glue to protect the marks from deterioration. When the glue had dried, the snail was returned to its capture location. Subsequent recaptures were only sightings, and further handling of the snail was unnecessary.

The punch-out method of marking (Barry Smith, University of Guam) we used resulted in a very low tag-loss rate (< 0.01 per month), which is necessary to avoid biased parameter estimates (Henry & Jarne, 2007). These tags are also functionally identical to the plastic tags that proved most resistant to deterioration in a comparative study of different snail marking methods (Henry & Jarne, 2007). Tag-loss was recorded as snails showing either only residual glue on their shells or having only one punch-out present. With moderate recapture rates and low dispersal, it was usually possible to deduce the identity of individuals with missing tags at a later date by looking at the encounter histories of other snails.

Although Henry & Jarne (2007) highlighted the deterioration risks of using different colored paint dots, individual color-codes last at least one year in field studies (K. Hall, personal observation). Snails less than 7 mm in length

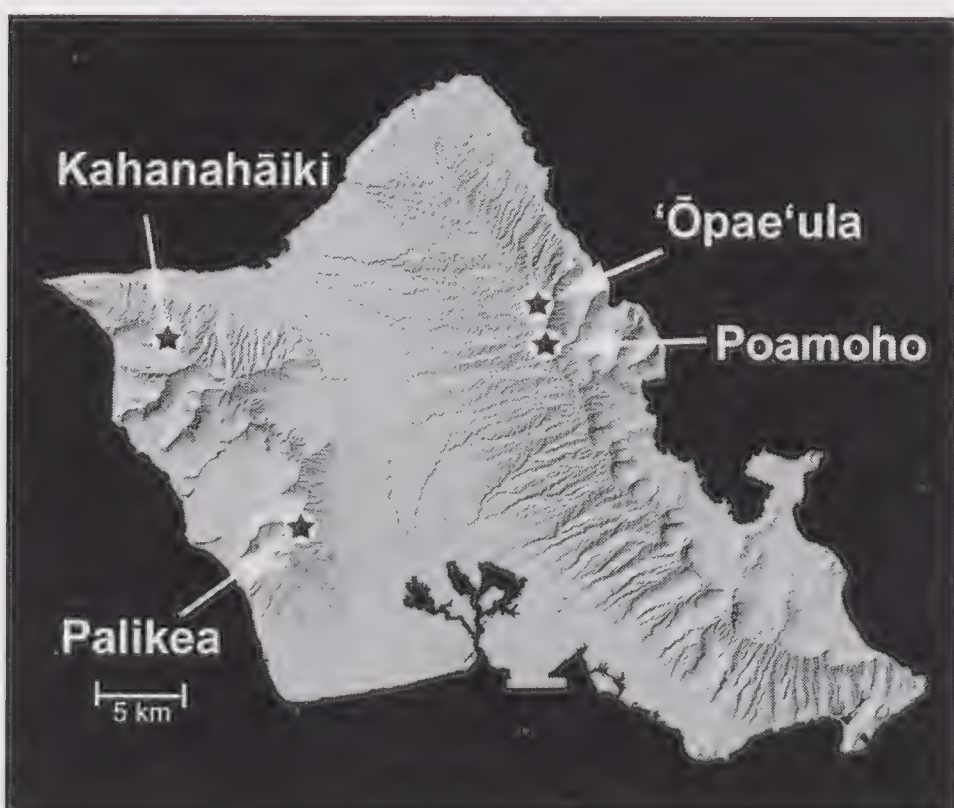


FIG. 1. The island of O'ahu. Points mark all four field site locations (courtesy of State of Hawai'i, Office of Planning).

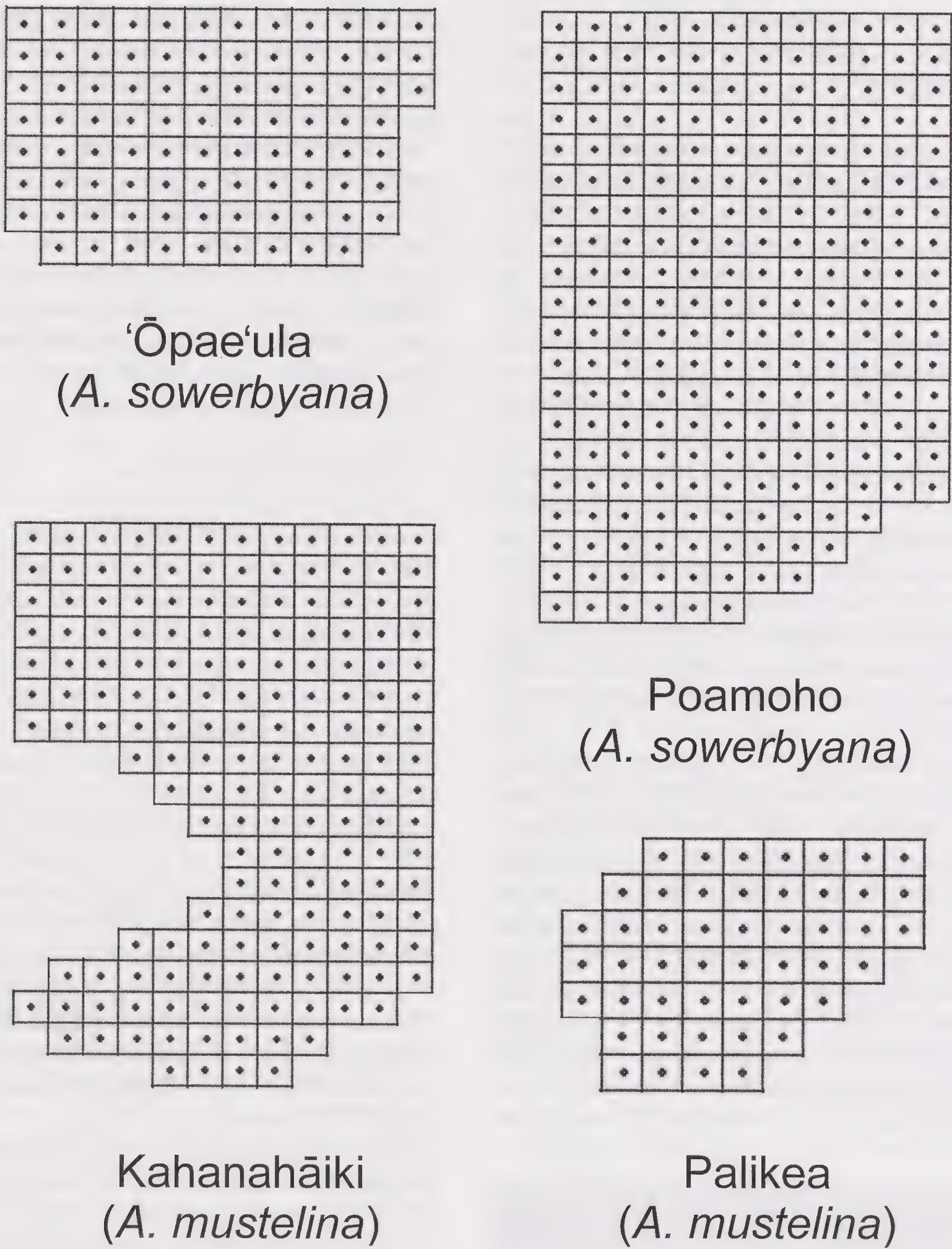


FIG. 2. Grid maps of the 4 sites used in this study. Each square quadrat represents 6.25 m².

received small circular dots using paint pens until they grew large enough to receive the paper marks. Using growth rate estimates (Hadfield et al., 1993) this can occur in less than one year even for the smallest sizes of juvenile snails.

Analysis of CMR Data

Model Structure – Each site was analyzed independently using a multi-strata design in Program MARK (White & Burnham, 1999)

to obtain simultaneous estimates of survival (φ), probability of capture (p), and probability of dispersal (ψ) parameters. To use Program MARK, one first needs to construct a global model. For each parameter, this linear model includes all variables under consideration that may have a significant effect on that parameter, including interactions. Reductions of the global model are then constructed based on plausible biological hypotheses, and reduced models are subsequently ranked to determine which hypotheses are best supported by the data.

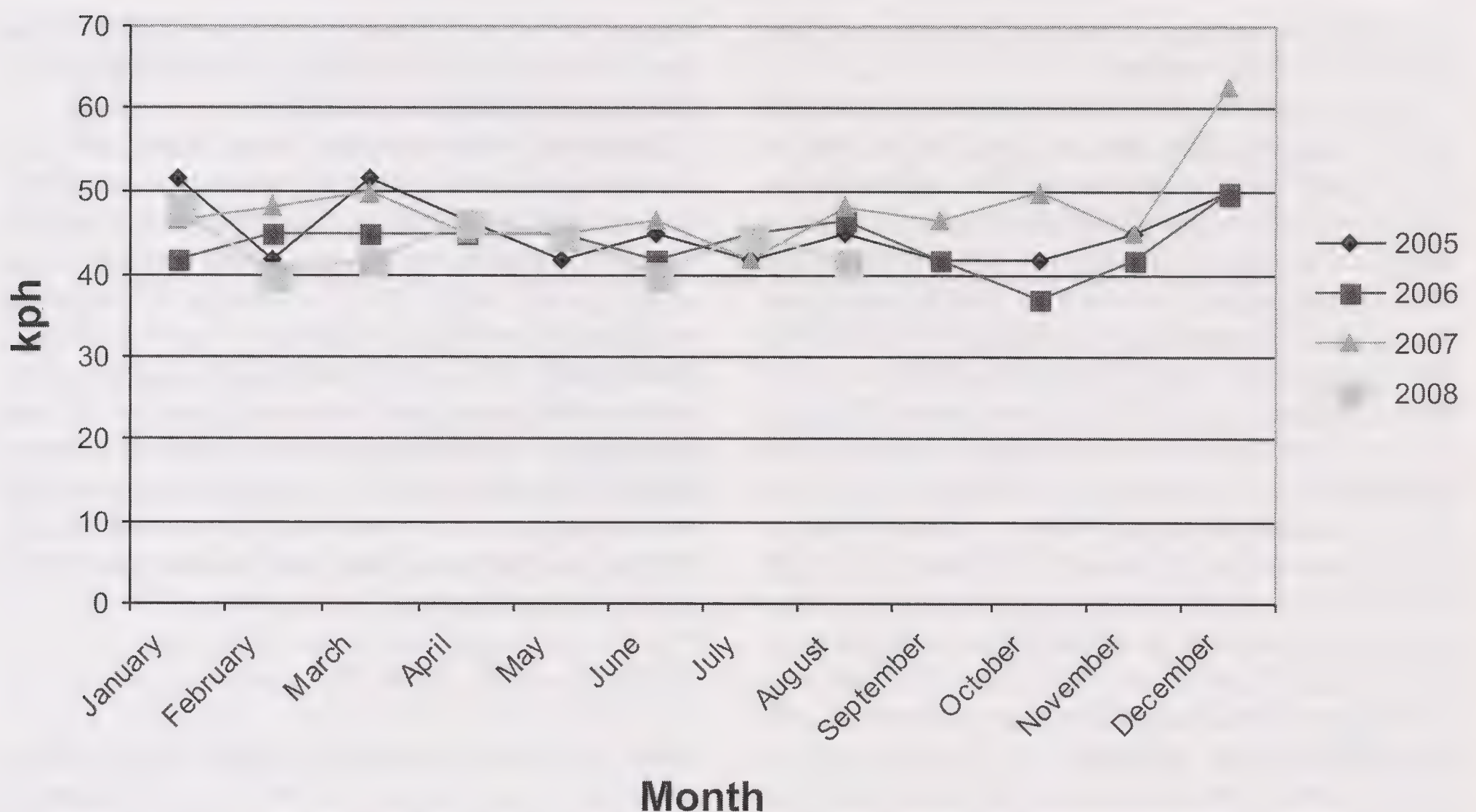


FIG. 3. Maximum monthly wind speed at HNL airport from January 2005 through August 2008.

An example of a reduced model using the conventional model notation (Lebreton et al., 1992) is $\phi(c)p(t*s)\psi(.)$, which means that survival (ϕ) was allowed to vary by variable c , capture probability (p) was allowed to vary by variables t and s (and their interaction), and dispersal (ψ) was constrained to a single parameter estimate. Full reduction of a parameter (no variation) is represented by $\phi(.)$, $p(.)$, or $\psi(.)$, with the most reduced model possible (only three estimated parameters) being $\phi(.)p(.)\psi(.)$.

The typical capture-history notation for multi-strata models uses letters to represent different locations (A, B, C, etc.) where an animal could be at a given time, and the model output is a series of ψ parameters to estimate the probability of transition between each pair of strata (locations) over a given time interval. We only estimated a *generic* dispersal parameter for each time interval (Zimmerman et al., 2007), because specific tree combinations were unimportant for calculating dispersal rates. These rates reflect the frequency that dispersal occurs; *distances* of such movements were analyzed separately.

Model Variables – Age was hypothesized to influence ϕ , p , and ψ . Three age-classes were designated, based on previous studies of *Achatinella* spp. that showed varying survival

between juveniles (0–1 years), subadults (1–2 years), and adults (2+ years) (Hadfield et al., 1993). Using growth measurements and modified logistic growth curves (Kaufmann, 1981; Hadfield et al., 1993), we assigned all snails in our study to one of these three age-classes at each time interval regardless of whether they were captured. A model containing $\phi(a)$, $p(a)$, or $\psi(a)$ would simply mean that survival, capture, or transition probability was allowed to vary among these three age categories in that model ($\phi(a)$ means three ϕ parameters were estimated, one for each age-class). Age-classes were also combined to reduce the number of parameters in some models, such as $\phi(\text{juv/non})$, which constrains ϕ to a juvenile (1st year) estimate and an “all other ages” estimate.

Temporal influence was suspected in survival and capture probabilities, which are represented by the $\phi(t)$ and $p(t)$ model notations, respectively (8–11 ϕ or p parameters estimated, according to the number of between-survey intervals at each site). Transition probability was only allowed to vary with time around the December 2007 interval (model notation $\psi(\text{dec07})$), when the highest winds between 2005 and 2008 were recorded (United States Weather Bureau, 2008) (Fig. 3). Based on Hall & Hadfield’s (2009) suggestion of a wind-dispersal mechanism for *Achatinella* spp., we assumed that if any major wind influence on ψ

would be detectable, it would be following the December 2007 storm.

Tree location (stratum) was not expected to have any effect on survival or transition probability. Since we were only estimating a single generic movement parameter, our three different strata (A, B and C) only represented “same tree as last survey”, “dispersal to flagged tree”, and “dispersal to un-flagged tree”. This last distinction was to address a known bias in recapture probability; trees were flagged in the field for reference when snails were captured, but snails have a strong preference to rest subsequently on flagging tape. Thus, a single tree could represent both strata A and B at the same time (and maybe C in a previous interval) – letters merely denote whether or not a snail had moved and the presence/absence of flagging. However, since C represents a tree without flagging, differences in capture probabilities were anticipated from those of A or B (previously flagged trees). Models with $p(s)$ denote that capture probability was allowed to vary between 2 groups (C and A+B); no models contained $\phi(s)$ or $\psi(s)$.

Model Selection and Parameter Estimation – A set of candidate models was created to compare varying hypotheses, each testing various combinations of variables on our three parameters of interest (ϕ , p , and ψ). All models tested were reductions of that site’s global model, as is required for such comparisons. Based on the variable descriptions above, the global models’ structures included interactions among all age-class categories (juvenile, subadult, adult) and between eight and eleven survey intervals (depending on the site) for ϕ ; age-class, strata, and time interval for p ; and age and weather for ψ . Program MARK uses Akaike’s Information Criterion (AIC – Akaike, 1974) to then rank reduced models by their relative likelihoods, and determine which model structures are most supported by the data provided.

To account for any overdispersion in our data, we tested the goodness of fit for our global models first. We chose the median c-hat approach implemented in Program MARK, which is the most appropriate test when the global model is not fully time dependent (Cooch & White, 2007: 5–29). The resulting variance inflation factor (c-hat) was used to adjust the model rankings in Program MARK. Model rankings that are adjusted for c-hat and sample sizes are denoted by QAICc (quasi-likelihood)

rather than AIC (Cooch & White, 2007). The top ranking models at each site correspond to the lowest QAICc values.

Dispersal and survival rates were not obtained directly from the top model (lowest QAICc), since no site’s top model received more than 75% support relative to other models. This support was measured by the w_i ’s (the Akaike weights, normalized so they sum to 1 for the model set). Uncertainty in model selection was addressed using a technique known as “model averaging” (Anderson, 2008) within Program MARK. Model averaging weighs each model according to its w_i , then provides a single estimate for the parameter and associated 95% confidence interval.

Emigration Simulation

To estimate emigration rates, we used a simulation technique that had been used previously with birds (Baker et al., 1995; Sharp et al., 2008). Limitations of such methods can be substantial for highly mobile species (Koenig et al., 2002), which tree snails are not. We first corrected our observed dispersal distance distributions for those dispersal events we missed due to emigration. This was done by simulating the entire range of observed dispersal distances from each quadrat in all directions, and then determining the proportion of simulated post-dispersal positions that occurred outside the boundaries of the site.

For each dispersal distance (in one-meter intervals), we used the ratio of off-site/on-site post-dispersal positions to provide a less biased frequency of that distance. As an example, if during simulation, 50% of all ten-meter dispersal events resulted in positions off-site, then we would have underestimated the frequency of ten-meter dispersers during our field studies by 50%. Thus, if we had observed eight ten-meter dispersers during field studies, the corrected frequency would now be 12 (= eight observations + 50% underestimate correction).

We then reran the simulations (50,000 iterations) using the corrected dispersal distributions, to again determine the proportion of all simulated post-dispersal positions that occurred outside the boundaries of each site. Proportions were calculated for every quadrat within the grids (Fig. 2). Values from all quadrats were then averaged to obtain a single proportion for each site. These proportions allowed us to estimate emigration rates. We assumed that we underestimated our uncorrected dispersal

rates (obtained using Program MARK) by an amount equivalent to these off-site proportions. Emigration was calculated by multiplying the off-site dispersal proportion by the uncorrected dispersal rate. For instance, a site with an average simulated off-site proportion of 40% and an uncorrected dispersal rate of 10% would have an emigration rate of 4% (40% x 10%).

Accounting for emigration allowed us to reduce bias in our original estimates of dispersal and survival. Corrected dispersal rates were obtained by adding the emigration rate directly to the original, uncorrected dispersal rate. Our original survival estimates also suffered from underestimation by not addressing emigration. To obtain less biased estimates of survival, we re-reran our MARK analyses including a fourth transitional stratum, U , which was set equal to the emigration rate of the site. Corrected estimates of survival were obtained from these models.

Application to Management

Calculating a suitable number of immigrants and emigrants for active conservation management requires knowing the density of the population, the dimensions of the proposed or existing reserve, and the average level of emigration expected from a reserve of those dimensions. Estimates of abundance were obtained by utilizing the Lincoln-Peterson estimator (Chao & Huggins, 2005). As described in the "Data Collection" section, an intensive survey was conducted at each site on one day, followed by a repeat of the same survey on the following day. This allows these nocturnal snails to re-mix within their host trees (< 3 m in height) overnight (Hall & Hadfield, 2009). By multiplying the reserve's simulated emigration rate (percent of population per month) by the number of animals present (population density x reserve dimensions), one can approximate the historical level of gene flow across the reserve boundaries. An example using data from Palikea is discussed to illustrate this application.

RESULTS

Model Averaging and Parameter Estimates

Goodness-of-fit tests (using median c -hat procedures) indicated that the global models provided adequate fits to the data with minimal

overdispersion. C -hat adjustments of 1.19, 0.98, 1.18 and 1.35 were made to 'Ōpae'ula, Poamoho, Kahanahāiki, and Palikea, respectively, before model selection began. These adjustments inflate sampling variances, which leads to a lower risk of falsely identifying a factor as important in a model. Table 1 shows the model rankings for each site based on QAICc criteria; top models are those with the lowest QAICc. Only the top four models at each site are presented, which includes all models with at least 10% support according to w_i 's.

For sites where age-varying models of survival were among the top two models ('Ōpae'ula and Kahanahāiki), model averaging was used to provide age-specific survival rates; otherwise a single survival parameter was estimated (Table 2). Also included in Table 2 are the corrected estimates of survival obtained by incorporating emigration; most estimates show significant increases as expected. Those estimates that showed decreases were both juvenile estimates, which already suffered from large standard errors and are unreliable.

Detection probabilities varied temporally (two-person surveys vs. the final four-person survey) at all sites except Palikea, which has nearly 75% less area included in the study grids making it easier to survey. Additional effort thus had little effect on the already high capture rates. Detection also varied with age and strata at two sites each (Table 1). At these sites, older (larger) snails and individuals in flagged trees were recaptured more often. More than 20 p parameters were estimated because of interactions among variables in top models; differences in sites' recapture rates are thus more easily displayed by analyzing raw data. Over 1,000 snails were captured and marked (394 at 'Ōpae'ula; 124 at Palikea, 226 at Poamoho, and 314 at Kahanahāiki). The average number of times a snail was recaptured was 0.95 ± 1.06 , 1.31 ± 1.92 , 0.79 ± 1.07 , and 1.23 ± 1.88 , in the same order. Both *A. mustelina* populations had the highest recapture rates; a frequency distribution of individual recaptures is provided in Figure 4.

Dispersal increases were detected after the December 2007 storm at every site in at least the 2nd best model, including the best model for Poamoho (Table 1). These dispersal rate estimates (percent of snails dispersing per month) are provided in Table 3. Distributions of observed (uncorrected) dispersal distances are shown in Figure 5, most were less than 10 m. Longer distances (> 20 m) were recorded

TABLE 1. Top four models at each site, ranked according to QAICc values. Δ QAICc is the difference in QAICc from top model, w_i denotes Akaike weight, Np is the number of estimable parameters in each model, and QDeviance (a major determinant of QAIC) is each model’s deviance after adjusting for overdispersion.

Species	Site	Model	QAICc	Δ QAICc	w_i	Np	QDeviance
<i>Achatinella sowerbyana</i>	Poamoho	$\phi(.)p(t)\psi(\text{dec07})$	956.33	0	0.74	6	429.91
		$\phi(.)p(t)\psi(.)$	959.63	3.29	0.14	5	435.29
		$\phi(.)p(t)\psi(a)$	961.21	4.88	0.06	6	434.79
		$\phi(\text{adult/non})p(t)\psi(.)$	961.59	5.26	0.05	6	435.17
	'Ōpae'ula	$\phi(a)p(t^*s)\psi(.)$	1,293.98	0	0.48	10	505.60
		$\phi(a)p(t^*s)\psi(\text{dec07})$	1,295.09	1.11	0.27	11	504.60
		$\phi(.)p(t^*s)\psi(.)$	1,295.74	1.77	0.20	8	511.55
		$\phi(a^*t)p(a^*t^*s)\psi(\text{dec07})$	1,298.77	4.79	0.04	24	479.84
	Palikea	$\phi(.)p(a^*s)\psi(.)$	562.49	0	0.37	8	343.00
		$\phi(.)p(a^*s)\psi(\text{dec07})$	563.56	1.08	0.21	9	341.92
		$\phi(\text{adult/non})p(a^*s)\psi(.)$	564.12	1.63	0.16	9	342.48
		$\phi(\text{juv/non})p(a^*s)\psi(.)$	564.55	2.06	0.13	9	342.91
	Kahanahāiki	$\phi(\text{juv/non})p(a^*t)\psi(.)$	1,648.62	0	0.33	12	821.78
		$\phi(\text{juv/non})p(a^*t)\psi(\text{dec07})$	1,650.05	1.43	0.16	13	821.11
		$\phi(.)p(a^*t)\psi(.)$	1,650.22	1.59	0.15	11	825.45
		$\phi(a)p(a^*t)\psi(.)$	1,650.49	1.87	0.13	13	821.56

at all sites except Palikea, which is smaller in area. Regression analyses of the relationship between dispersal interval (days between observations) and distance traveled indicate that longer movements are not exclusively sums of successive shorter movements. R^2 values were 0.2% ($p = 0.76$), 34% ($p = .01$), 0.7% ($p = 0.76$), and 1% ($p = 0.65$), for 'Ōpae'ula, Poamoho, Kahanahāiki, and Palikea, respectively. Although the Poamoho relationship appears significant, removal of two extreme outliers changes the relationship ($R^2 = 4\%$, $p = 0.14$) to a similar level as recorded elsewhere. This implies that, for the most part, longer dispersal distances can be either single movements or

a sum of successive movements. Additionally, some short distances can be a sum of return movements or just a single movement.

Emigration Simulation and Dispersal Correction

Our simulations rested upon assumptions of non-preference for dispersal direction, independence of successive movements, and equal potential for dispersal from any point within the site. We tested preference for one or more directions of movement using the Rayleigh test (Zar, 1984), in which the null hypothesis is no preference for directionality. Random directionality was confirmed at 'Ōpae'ula (61

TABLE 2. Uncorrected monthly survival rates, age-specific where available, with associated standard errors (SE) and 95% confidence intervals (LCI - lower 95% boundary, UCI - upper 95% boundary). Corrected rates, which account for emigration, are listed in the final columns. Means are percentages of population surviving per month. Annual survival is calculated by raising the mean monthly survival estimate to the 12th power; data were insufficient to support a model with varying survival among any age groupings at Poamoho and Palikea.

Species	Site	Age Class	Mean	SE	LCI	UCI	Annual Survival	Corrected Mean	Corrected Annual Survival
<i>Achatinella sowerbyana</i>	Poamoho	-	0.929	0.010	0.907	0.946	0.413	0.938	0.464
	'Ōpae'ula	Juvenile	0.941	0.021	0.831	0.981	0.482	0.934	0.441
		Subadult	0.983	0.011	0.935	0.995	0.814	0.987	0.854
		Adult	0.978	0.006	0.958	0.989	0.766	0.982	0.804
<i>Achatinella mustelina</i>	Palikea	-	0.942	0.011	0.915	0.96	0.488	0.956	0.583
	Kahanahāiki	Juvenile	0.901	0.019	0.819	0.948	0.286	0.891	0.250
		Non-juv	0.934	0.007	0.888	0.962	0.441	0.941	0.482

movements total, $p = 0.47$), Poamoho (30, $p = 0.62$), Kahanahāiki (15, $p = 0.87$), and Palikea (23, $p = 0.32$). It was uncommon to observe a snail dispersing more than once, so analyses of autocorrelation with regards to dispersal direction were not possible. We also found no association between any portion of a site and increased dispersal.

The probability of missing a dispersal event increased with distance of dispersal. During simulation of distances of 1–30 m from all points on the grids, shorter distances (1–3 m) remained within the grid as frequently as 90%. Longer distances in excess of 20 m ended up within the grid less than 10% of the time. To obtain the corrected dispersal distributions (Fig. 5), we simply divided the frequency of each observed dispersal distance by the frequency of detection on the grid during simulation. To illustrate, there were eight observations of 6-meter dispersal during field studies at 'Ōpae'ula, and 6-meter dispersal resulted in on-grid positions in 70% of simulations. Dividing 8 by 0.7 gives us the corrected frequency of ~ 11.

Provided that a dispersal event has occurred, the proportions of simulated dispersal events that end outside the study site boundaries are provided in Figure 6 for each origin point on the grid. These proportions were weighted by the frequency of occurrence, and then averaged to obtain a single proportion for each site. Average proportions were 0.394, 0.284, 0.354 and

0.494 for 'Ōpae'ula, Poamoho, Kahanahāiki, and Palikea, respectively.

To calculate emigration rates, we multiplied these proportions by our uncorrected dispersal rates, resulting in emigration rates of 0.067, 0.018, 0.007, and 0.046 in that same order. Corrected dispersal rates were obtained by adding emigration rates to our uncorrected dispersal rates, all of which are summarized in Table 3. Survival rates were corrected by running Program MARK with the emigration stratum, U . In most cases, this re-analysis significantly increased our estimates of survival (Table 2).

The two-day surveys in August 2008 provided adult abundance ($\pm$ standard error) estimates of 191 (± 20), 74 (± 16), 53 (± 4), and 25 (± 3) for 'Ōpae'ula, Poamoho, Kahanahāiki, and Palikea, respectively. The areas of each site (Fig. 2) were 550, 1388, 975, and 275 m², in that same order, corresponding to densities of 0.34, 0.05, 0.05, and 0.09 snails/m². We can use Palikea as a practical example of the translocation application by assuming an enclosure was to be erected around the site perimeter delineated in Figure 2. Abundance was estimated at 25 adult snails, and multiplying 25 by the emigration rate of 0.046, we get ~ 1 migrant per month. On an annual basis, this translates to 12 migrants per year to translocate from surrounding populations into the reserve, and vice versa.

DISCUSSION

Survival Rates

Age-class effects on survival were apparent for only Kahanahāiki and ‘Ōpae‘ula, although the other sites probably follow the same trend (Hadfield et al., 1993). Very few juvenile snails were recaptured at Poamoho and Palikea, so those survival estimates reflect mostly the adult individuals. Annual survival rates at Kahanahāiki (before accounting for emigration, Table 2) closely matched the estimates of Hadfield et al. (1993), which were obtained from a conspecific population located 200 m away. This further strengthened confidence in using our new methods to estimate survival at other sites.

Juvenile survival was, as in Hadfield et al. (1993), found to be nearly half that of the non-juvenile survival rates when comparison was appropriate (Table 2). Survival was clearly highest for all age groups at ‘Ōpae‘ula. Not coincidentally, this is also the only site where the predatory snail *Euglandina rosea* has yet to be seen. Rats and *E. rosea* are both present at the other three sites, and survivorship is similar among

them. These data suggest that predator control efforts should be increased at these three sites, until survival rates approach levels at ‘Ōpae‘ula. Survival rates did not significantly vary with time at any site, supporting the notion that massive predator influxes (as in Hadfield et al., 1993) did not occur during our study, but rather that predation pressure may be constant.

Recapture Rates

As expected, both Palikea and ‘Ōpae‘ula showed increased recapture probabilities in previously flagged trees, which is evident by the $p(s)$ parameters in both sites’ top models (Table 1). Kahanahāiki did not reveal this same pattern, probably because most trees were flagged early in the study, leaving few data available to estimate any un-flagged tree parameters. It was not surprising that Poamoho also did not show this pattern; flagging is quickly destroyed by the constant and fierce winds to which that site is exposed. Detection probability increases among larger age-classes were intuitive, as were increases due to increased search effort.

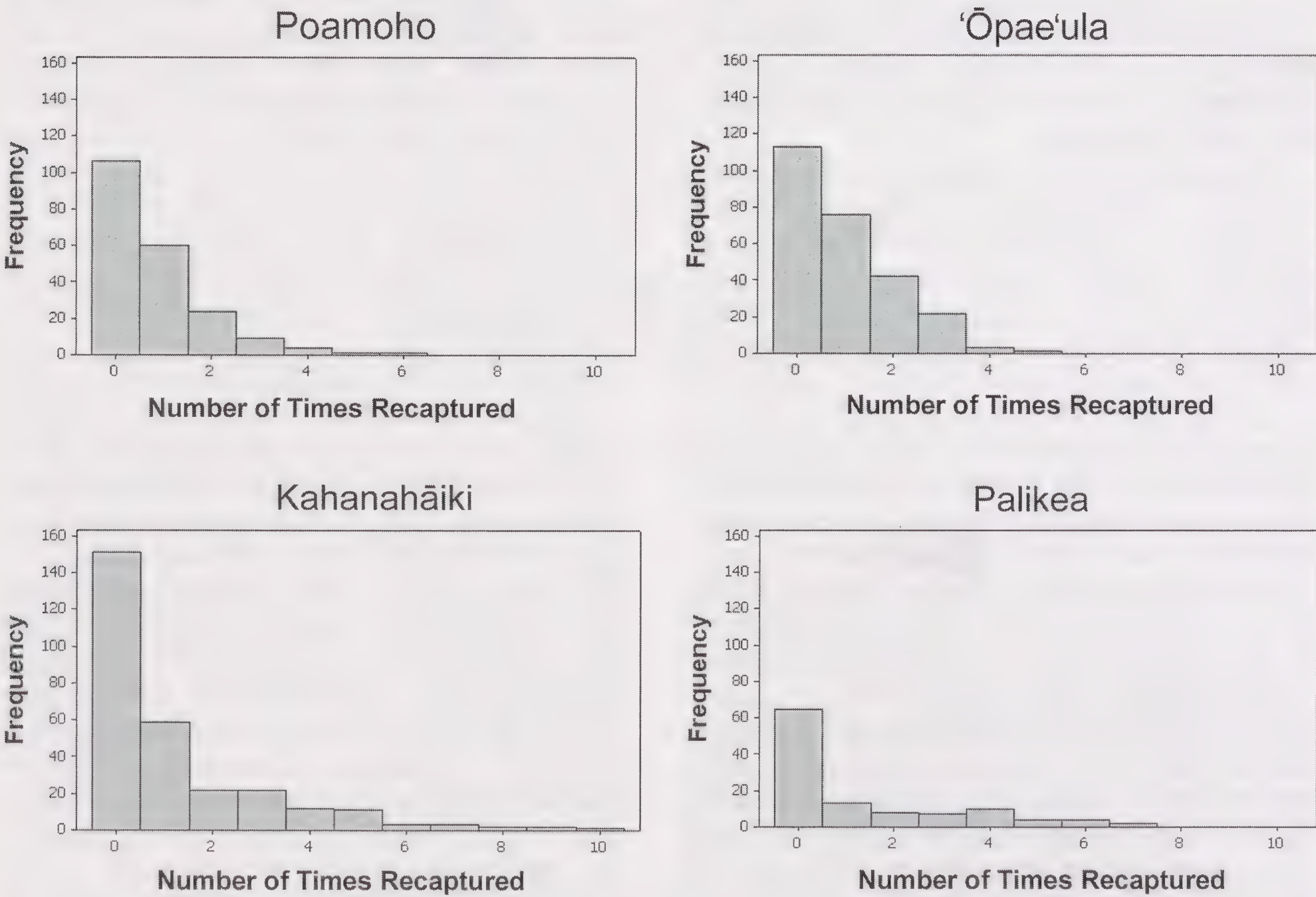


FIG. 4. Histogram showing the frequency of snails being recaptured X number of times at each site (*A. sowerbyana* – top panels, *A. mustelina* – bottom panels).

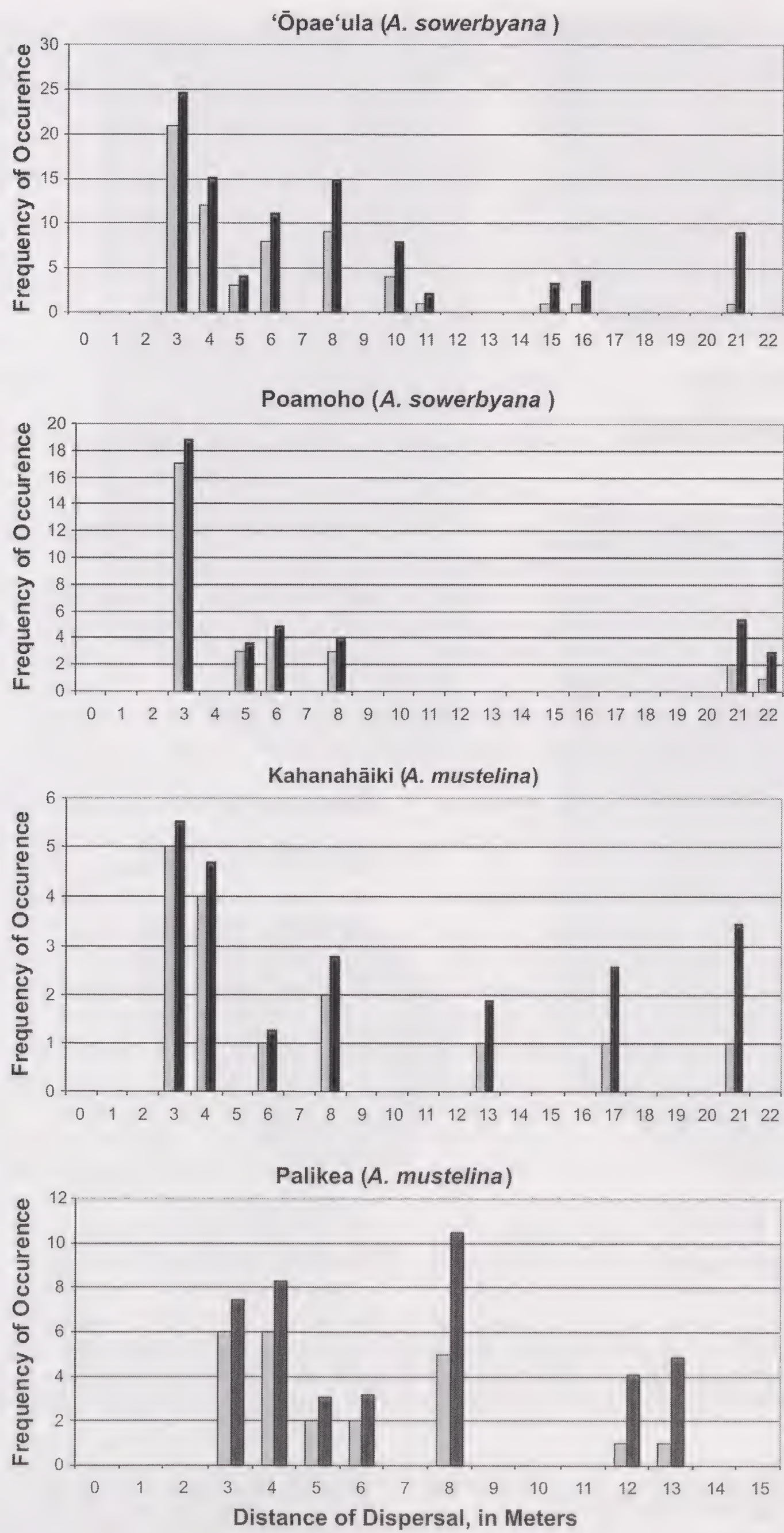


FIG. 5. Uncorrected and corrected distributions of snail dispersal distances, by site, from 2005 through 2008. Gray bars indicate the actual frequency of observed dispersal distances (uncorrected). Black bars represent the results of simulations, which include non-observable emigration (corrected).

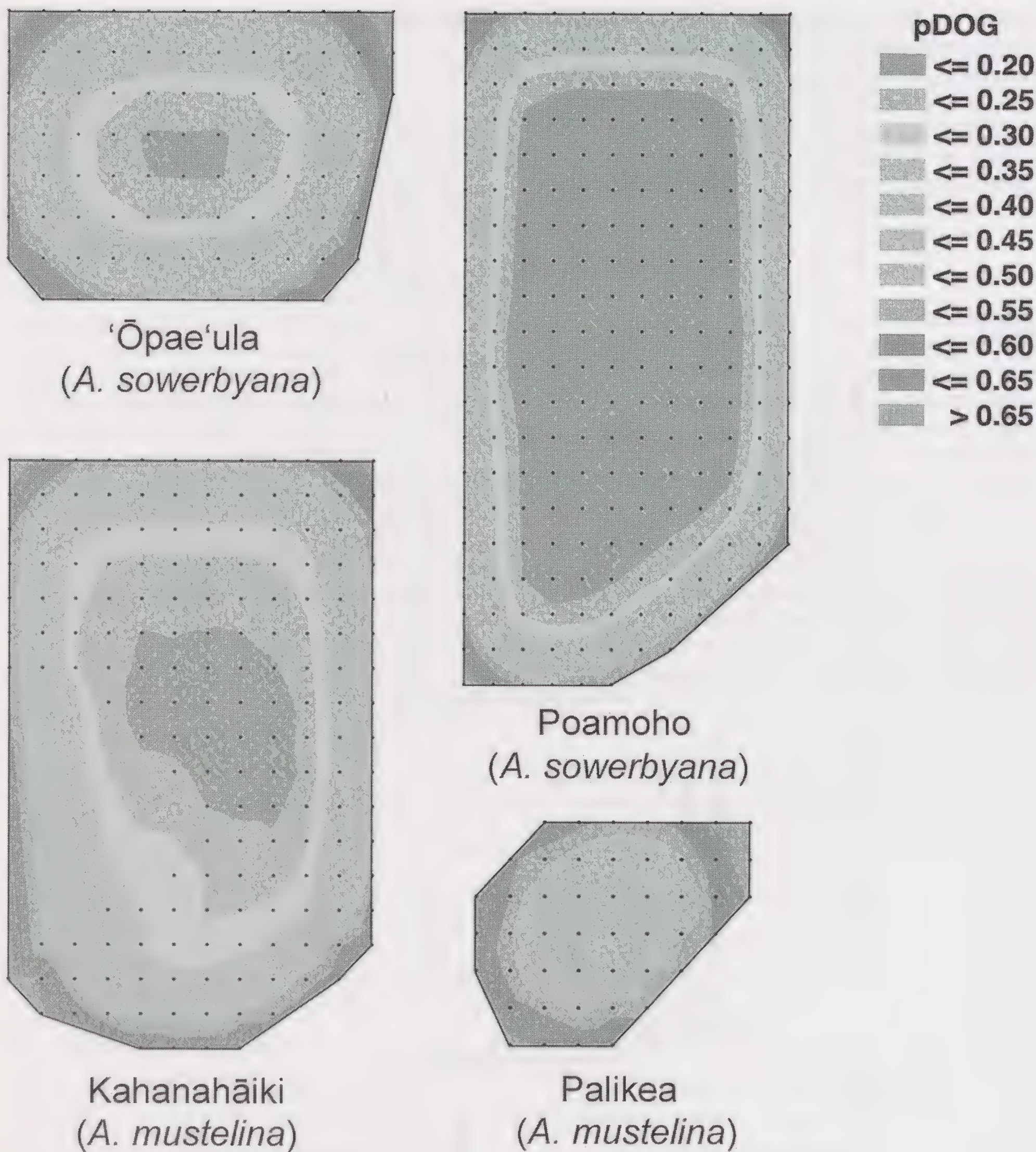


FIG. 6. Probability that random-direction dispersal events, sampled from simulated distributions of distances at all points on the grid, will end up beyond the boundaries of the study sites. pDOG is the probability of dispersal off-grid; lower values of pDOG are found in the center of the site.

Recapture proportions (Fig. 4) reflected the relative exposure of each site to inclement weather. In decreasing order from least exposure to greatest are Kahanahāiki, Palikea, Opae'ula, and Poamoho (Hall & Hadfield, 2009). The two lowest recapture proportions were both from *A. sowerbyana*, which occurs in the Ko'olau Mountains where wind

speeds are more extreme. This pattern was not surprising because dispersal and emigration are increased in areas of high wind (Hall & Hadfield, 2009), and surveys are difficult in areas with severe weather. In contrast, many *A. mustelina* were recaptured multiple times at the two Wai'anae sites (Fig. 4) where weather conditions are more benign.

TABLE 3. Summary of emigration and dispersal rates at all four sites. Corrected dispersal rates are calculated by adding uncorrected dispersal rates to emigration rates, which are themselves a product of off-site proportions and uncorrected dispersal rates. Parentheses for Poamoho rates indicate the increased rates from the December 2007 storm.

Species	Site	Uncorrected dispersal rate	Off-site proportion	Emigration rate	Corrected Dispersal rate
<i>Achatinella sowerbyana</i>	Poamoho	0.063(0.119)	0.284	0.018	0.081(0.137)
	‘Ōpae‘ula	0.169	0.394	0.067	0.236
<i>Achatinella mustelina</i>	Palikea	0.093	0.494	0.046	0.193
	Kahanahāiki	0.020	0.354	0.007	0.027

Dispersal Rates and Distances

Transition probabilities did not differ among age groups, but again, this could be because of low recapture rates of juveniles (and even fewer records of juvenile movement). All sites showed some effect from the December 2007 storm in at least the 2nd best model, and Poamoho showed a substantial increase in dispersal following the storm in its top model. Poamoho is exposed to winds far more than any other site (Hall & Hadfield, 2009), which may provide an explanation as to why only this one site revealed such a strong effect. Long-term weather records (United States Weather Bureau, 2008) will further assist conservation managers in guiding episodic translocation rates for this population, based on the frequency of severe storms.

‘Ōpae‘ula had a substantially higher rate of dispersal than any other site, possibly due to its exposure to both easterly and westerly wind gusts along an exposed Ko‘olau ridge. Poamoho has even more extreme exposure to NE trade-wind gusts, so it is unclear why ‘Ōpae‘ula would show higher rates. Kahanahāiki had a significantly lower rate of dispersal than all other sites, possibly because of its dense, tall vegetation (Cowie, 1980) and location being set back from an exposed ridge. Wind speeds have been recorded at all sites and Kahanahāiki was consistently the calmest (Hall & Hadfield, 2009). Palikea and Poamoho (not including the December 2007 effect) had nearly identical dispersal rates, and have similar ridgeline locations. There does not appear to be a species effect on dispersal rates, which seem to be dependent primarily on site location and exposure to inclement weather.

The dispersal estimates of this study are in close agreement with preliminary estimates obtained using radar tracking techniques (Hall & Hadfield, 2009). In that study, monthly dispersal rate estimates were 0–20%, which is similar to the 3–24% in this study (Table 3). Radar tracking also revealed an average monthly dispersal distance of 4.94 m, similar to that observed using CMR (5.25, 5.50, 6.39 and 5.12 m for ‘Ōpae‘ula, Poamoho, Kahanahāiki, and Palikea, respectively, Fig. 5).

Management Implications

To mimic natural gene flow across reserve boundaries, we recommend a rate of exchange between neighboring populations analogous to simulated emigration rates corresponding to relevant reserve dimensions. This rate should be equal for the number of adults moved both into a reserve and out of the reserve. The tree snail system provides a simplistic example with which to illustrate this approach, owing to the species’ short dispersal range and small reserve (exclosure fence) sizes. Our proposed methods should require minimal modification for use with larger and more vagile species in larger reserves, where rather than fences, reserve boundaries might be roads or other inhospitable landscapes.

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PERI-TYRRHENIAN PHYLOGEOGRAPHY IN THE LAND SNAIL
SOLATOPUPA GUIDONI (PULMONATA)

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ABSTRACT

The land snail *Solatopupa guidoni* has an interesting disjunct distribution in the peri-Tyrrhenian area, with a few scattered populations in Sardinia, Corsica, and Elba Island. The species is strictly bound to limestone and has poor dispersal capacity. Here, we used sequences of two mitochondrial genes, cytochrome oxidase I (COI) and 16S rRNA (16S), to reconstruct the species phylogeography. The study is based on nine of the 13 populations reported in the literature. Phylogenetic methods and nested clade analysis failed to retrieve reciprocally monophyletic lineages on each island. Sardinian and Elba Island populations were found to be embedded within those of Corsica. These results contrast with previous phylogeographic studies of other organisms with similar distribution patterns, showing major phylogeographic breaks between islands. Molecular clock estimates suggest that species diversification occurred less than 2.5 Myr ago, in line with a previous study that dated the split of *S. guidoni* from its continental sister species at 3–5 Myr. Corsican populations can be tentatively sorted into two haplo-groups. A first group includes haplotypes found in central inland Corsica only, whereas haplotypes found in northern coastal locations cluster in a second haplo-group. The latter also includes Sardinian and Elba Island populations. Molecular data indicate that a combination of vicariance and dispersal events provide the best explanation of the distribution of this species.

Key words: *Solatopupa*, land snail, phylogeography, COI, 16S, Nested Clade Phylogeographical Analysis, molecular clock.

INTRODUCTION

The genus *Solatopupa* Pilsbry, 1917, comprises a small group of six land snail species with a peri-Tyrrhenian distribution, ranging from northern Spain to central Italy, including Sardinia, Corsica, and Elba Island. All but one species (*S. cianensis*) ascribed to the genus are strictly bound to limestone. These characteristics, coupled with the general low potential for long-distance dispersal of land snails, make *Solatopupa* a reliable model for biogeographic studies. The distribution of the genus has been traditionally explained by vicariance due to paleogeographic events that caused the detachment of the Sardinia-Corsica microplate from the Iberian plate in the early Oligocene, its subsequent rotation anti-clockwise towards the Italian peninsula (early to middle Miocene), and finally its separation into two islands (Alvarez, 1972; Bellon et al., 1977; Boccaletti et al.,

1990; Carmignani et al., 1995; Gelabert et al., 2002; Bosellini, 2005). The interaction of the microplate with the emerging Apennine chain during the Pliocene has been invoked to explain the occurrence of a single species, *Solatopupa guidoni* (Caziot, 1902), in Sardinia, Corsica, and Elba Island (Giusti, 1977).

Ketmaier et al. (2006) produced a phylogenetic hypothesis for the genus *Solatopupa* based on nucleotide sequences of three mitochondrial and one nuclear gene, showing that phylogenetic relationships were consistent with the paleogeography of the peri-Tyrrhenian area. However, contrary to previous reports on other taxa with similar peri-Tyrrhenian distributions, molecular clock estimates suggested that the diversification of *Solatopupa* coincided with the very last phases of detachment of the microplate (late Miocene-middle Pliocene) rather than with the initial ones (late Oligocene-early Miocene). Molecular data also suggested that

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the relatively widespread *S. similis* (Bruguière, 1792), occurring from northern Spain to eastern Liguria, Italy, is the continental sister species to the exclusively insular *S. guidoni*. Ketmaier et al. (2006) analyzed four populations of *S. guidoni* (two from Corsica, one from Sardinia and one from Elba Island) and found a close affinity between the Sardinian and Elba Island populations, whereas the Corsican populations formed a single clade. Previous allozyme data on a slightly different set of populations suggested two genetically distinct lineages in the species ($F_{ST} = 0.523$ over 28 loci, $P < 0.05$; Boato, 1988; at that time, the name *S. simonetiae* was still used to identify the species, and only later was it synonymized with *S. guidoni*). One group comprised two populations from inland Corsica and one included two populations from northern coastal Corsica and one population from Sardinia.

Solatopupa guidoni has a very scattered distribution, with nine populations known from Corsica, two from Sardinia and two from Elba Island (Fig. 1; Giusti, 1977). Populations are strictly associated with calcareous rocks; these are of different ages in the case of Corsica and Sardinia (Fig. 1). For this study, we considerably expanded the sampling in terms of populations and individuals, and we sampled nine out of the 13 known populations and surveyed a total of 60 individuals. We could not find any individual in four other localities from which the species has been reported in the past (Fig. 1). We also surveyed other ecologically suitable areas (i.e. with limestone), particularly in central and southern Corsica but without success. It therefore seems likely that we covered the whole range of the species.

We used fragments of two mitochondrial DNA (mtDNA) genes – cytochrome oxidase I (COI) and 16S rRNA (16S) – to produce a phylogeographic hypothesis for *S. guidoni*. COI and 16S are the most variable genes sequenced by Ketmaier et al. (2006); we therefore expected to find sufficient genetic variation to clarify relationships at population level. We aimed to determine (1) whether mtDNA lineages occurring on the three islands are reciprocally monophyletic as expected in light of their allopatric distribution and the poor dispersal capacity of the species. We also want to (2) obtain an approximate temporal framework for the intraspecific diversification of the species. Because the split between *S. guidoni* and its closest continental relative *S. similis* has been dated at 3–5 Myr (Ketmaier et al., 2006), divergence in *S. guidoni* should be more recent.

Finally, we aim to exploit our wider sampling to (3) test the hypothesis of Boato (1988) that in Corsica *S. guidoni* would comprise two genetically distinct lineages. We discuss our findings in light of the paleogeography of the area and phylogeographic studies conducted on a variety of groups with peri-Tyrrhenian distribution (i.e. newts, subterranean terrestrial and aquatic isopods, stoneflies, and flightless beetles) (Cobolli Sbordoni et al., 1995; Caccone et al., 1997; Ketmaier et al., 1999, 2000, 2003a, b; Fochetti et al., 2004).

MATERIALS AND METHODS

Sampling, DNA extraction, PCR Amplification and Sequencing

Five Corsican populations of *S. guidoni* were sampled, and this material was added to the four populations (one from Sardinia, two from Corsica and one from Elba Island) analyzed by Ketmaier et al. (2006). Details on sampling localities and sample sizes are given in Table 1 and Figure 1. Total genomic DNA was extracted following Ketmaier et al. (2006). We used the same primers and PCR conditions as in Ketmaier et al. (2006) to amplify about 700 and 500 base pairs (bp) of mitochondrial DNA (mtDNA) of Cytochrome Oxidase I (COI) and 16S rRNA (16S) gene fragments. PCR products were sequenced with an automated sequencer (Applied Biosystems 373A) following the manufacturer's protocols. To promote accuracy, both strands were sequenced using the primers employed for PCR. The sequences have been deposited in GenBank (Accession No. GU046364–GU046389; Table 1).

Population Genetics and Phylogenetic Analyses

Sequences were edited and aligned using Sequencher 4.6 (Gene Code Corporation); alignments were also checked by eye. The suitability of pooling sequence data from the two sequenced genes was assessed by the incongruence length difference test (Farris et al., 1994), as implemented in PAUP* 4.0β10 (Swofford, 2002). The test showed that the two regions are not phylogenetically incongruent ($P = 0.787$). We further check combinability by using the Bayesian approach detailed in Kauff & Lutzoni (2002), with a threshold value of posterior probabilities $\geq 99\%$ for conflicting relationships. None of the few conflicting relationships revealed by the separate analyses received reciprocal pos-

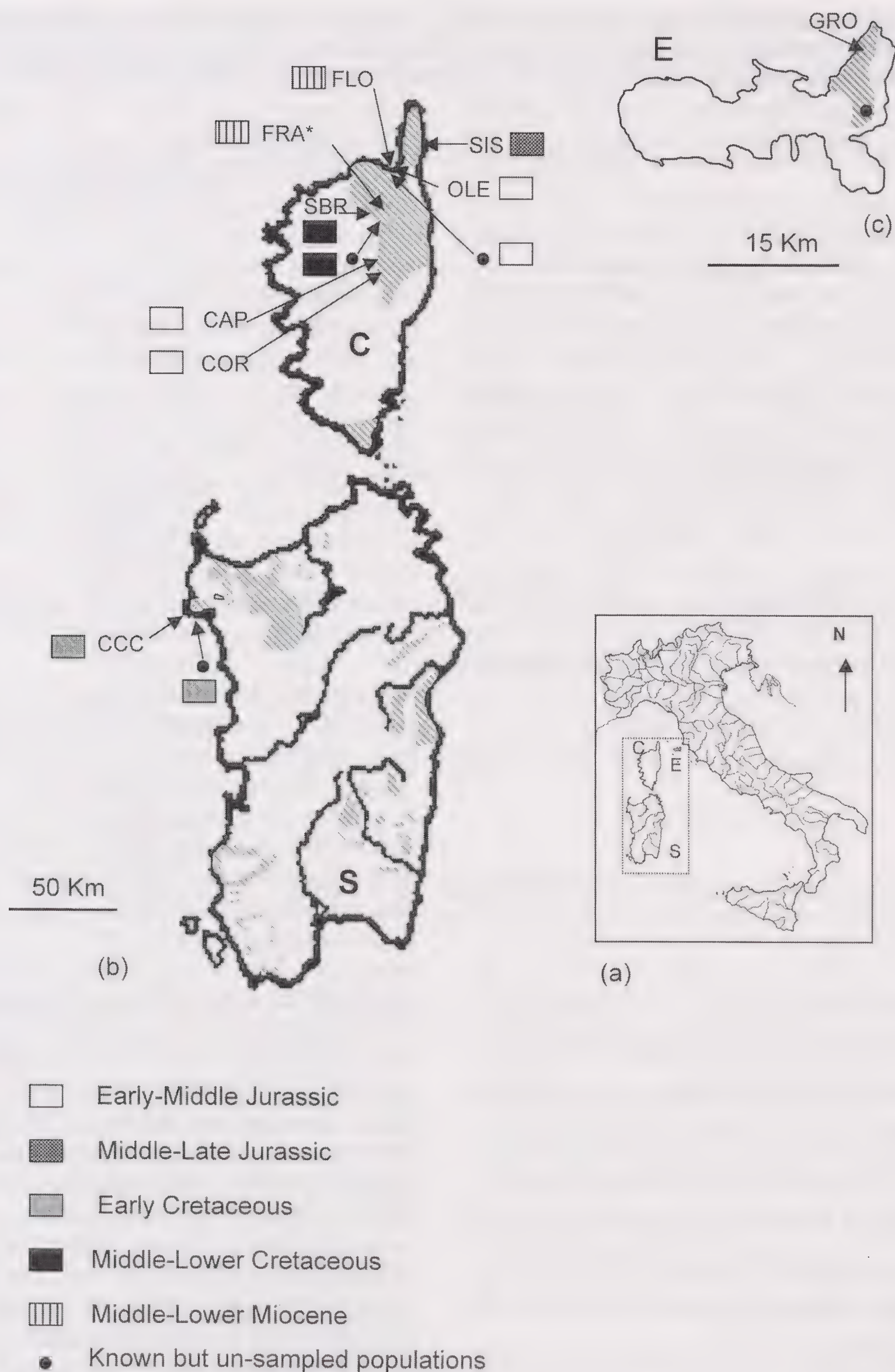


FIG. 1. Schematic maps showing the sampling localities of the *Solatopupa guidoni* populations included in the study and the geology of the region. (a) Geographic position of the three islands - Sardinia (S), Corsica (C), and Elba Island (E) - where *S. guidoni* occurs. In (b) and (c) are respectively shown sampling localities in Corsica/Sardinia and Elba Island. Three letter codes identify different populations and they correspond to those in Table 1. Black dots identify localities where the species had been reported but not found during our samplings. Downward diagonal shading indicates the distribution of limestone in three islands. Different patterned rectangles close to each population refer to the different ages of calcareous rocks inhabited by *S. guidoni* populations (this information is not available for Elba Island). Positioning of three islands roughly approximates real geographic relationships but sizes of the islands are not in proportion to one another (see scale bars).

TABLE 1. Locality, latitudinal and longitudinal data (Lat/Log) used in the nested clade analysis, sample size (N), and abbreviations for the *Solatopupa guidoni* populations included in the study. The last two columns report GenBank accession numbers. ^aAllozyme data from Boato (1988); ^bData from Ketmaier et al. (2006).

Locality	Lat/Long	N	Code	GenBank accession numbers	
				COI	16S
Capo Caccia, Sardinia, Italy	40°33'N, 8°9'E	3	CCC ^a	DQ305079 ^b	DQ305064 ^b
Corte, Corsica, France	42°18'N, 9°9'E	16	COR	GU046364	GU046381
				GU046365	GU046386
Sabara, Corsica, France	42°25'N, 9°8'E	4	SBR ^a	DQ305080 ^b	DQ305062 ^b
Francardo, Corsica, France	42°23'N, 9°11'E	3	FRA ^a	DQ305077 ^b	DQ305063 ^b
Caporalino, Corsica, France	42°22'N, 9°11'E	5	CAP ^a	GU046366	GU046379
				GU046367	GU046380
				GU046368	GU046385
				GU046369	
Oletta, Corsica, France	42°37'N, 9°20'E	9	OLE	GU046370	GU046384
				GU046371	GU046389
St. Florent, Corsica, France	42°41'N, 9°19'E	10	FLO ^a	GU046372	GU046382
				GU046373	GU046383
				GU046374	GU046387
Sisco, Corsica, France	42°48'N, 9°29'E	8	SIS	GU046375	GU046388
				GU046376	
				GU046377	
				GU046378	
Monte Grosso, Elba Island, Italy	42°51'N, 10°24'E	2	GRO	DQ305076 ^b	DQ305061 ^b

terior probabilities of $\geq 99\%$. In light of these results, we present only analyses based on the two genes combined. We used PAUP* 4.0 β 10 to calculate base frequencies and to test for base frequency homogeneity across taxa (χ^2 test). To detect saturation of substitutions, we plotted the absolute number of transversions and transitions against uncorrected-p genetic distances. This was done for each gene separately and for the two genes combined. For the COI dataset, saturation plots were derived for third codon positions only.

Data was analyzed phylogenetically with *S. similis* (GenBank Accession Nos. DQ305085 and DQ305059 for COI and 16S, respectively) as outgroup. This species is sister to *S. guidoni* in the genus phylogeny (Ketmaier et al., 2006). We used MODELTEST (Posada & Crandall, 1998) to determine the model of sequence evolution that best fit our data. We then used the MODELTEST output to calculate Maximum Likelihood (ML) genetic distances for Neighbor-Joining (NJ) analyses, as implemented in PAUP. We employed the same model of sequence evolution for Bayesian searches. These were run

in MrBAYES 3.0b4 (Ronquist & Huelsenbeck, 2003) allowing site-specific rate variation partitioned by gene and, for COI, by codon position. MrBAYES was run for two million generations with a sampling frequency of 100 generations. We ran one cold and three heated Markov chains and two independent runs. To assess if the Markov chains had reached stationarity, we plotted the likelihood scores of the sampled trees against generation time. Trees generated before stationarity were discarded as burn-in (first 10% of the sampled trees) and posterior probability values for each node were calculated on the basis of the remaining 90% of sampled trees. These trees were then used to construct a 50% majority rule consensus tree in PAUP. The robustness of the NJ tree was tested by 1,000 bootstrap replicates in PAUP. Phylogenetic tree topologies generated with different phylogenetic methods and competing phylogenetic hypotheses were evaluated statistically with the unbiased tree selection test (AU) as implemented in CONSEL (Shimodaira & Hasegawa, 2001). We compared tree topologies simultaneously (Shimodaira & Hasegawa, 1999).

The molecular clock hypothesis was tested with the likelihood ratio test (LRT; Goldman, 1993), which compares the log-likelihood of ML trees with and without assuming a molecular clock. Time estimates were calculated according to the formula $T = D_{ML}/2r$, where D_{ML} is the maximum likelihood genetic distance and r is the mutation rate. D_{ML} distances were calculated for the COI and 16S partitions separately using the substitution model parameters selected for each data partition with MODELTEST (Posada & Crandall, 1998). We used previous published rates for mollusks to derive divergence times; the same rates were adopted in Ketmaier et al. (2006). Thus, time estimates between that study and the current one are perfectly comparable. Rates vary between 0.67 and 1.21% per million years for COI and between 0.5 and 0.6% per million years for mitochondrial ribosomal genes (Ozawa & Okamoto, 1993; Rumbak et al., 1994; Marko, 2002).

We used the Nested Clade Phylogeographical Analysis (NCPA) (Templeton, 1998) to test for association between genealogy and geography in the dataset and to infer population processes. This method has been recently criticized, because it seems to be prone to a high rate of false positives (e.g. Knowles, 2008; Petit, 2008). However, NCPA has still a number of advantages compared to alternative methods (Templeton, 2009). In addition, we based our main conclusions on multiple independent analyses (i.e. phylogenetic and population genetics methods) to complement the NCPA inferences. We used the software ANeCA (Panchal & Beaumont, 2007), which automates the complex NCPA and renders manual procedures (i.e. the nesting design) in the analysis unnecessary. The package includes TCS, which implements the statistical parsimony procedure (Clement et al., 2000), and GEO-DIS (Posada et al., 2000) to respectively derive the haplotype network and to calculate distances among haplotypes and clades and their statistical significance. We included four additional locations in the GEODIS analysis (Monte Castello, Elba Island, 42°47'N, 10°22'E; Col de Teghime, Corsica, 42°40'N, 9°24'E; Sabara, Corsica, 42°24'N, 9°10'E; Punta Giglio, Sardinia, 40°34'N, 8°12'E; indicated by black dots in Fig. 1). These are localities where the species had been found in the past but not during our sampling; including this information is important to detect any sampling inadequacies (Panchal & Beaumont, 2007). The statistical

distribution of distances was determined by re-calculating distances after 10,000 random permutations (i.e., clades against sampling localities). ANeCA automatically runs a slightly different version of the inference keys, dated 14 July 2004.

We used ARLEQUIN 3.0 (Excoffier et al., 2005) to calculate the following parameters of genetic diversity for each population: haplotype diversity (h), mean number of pairwise differences between all pairs of haplotypes (π) and the nucleotide diversity (π_n). Levels of genetic diversity were tested by a hierarchical analysis of molecular variance (AMOVA) (Excoffier et al., 1992) in ARLEQUIN with 1,000 replications. For this analysis we grouped populations (1) by island of provenance, and (2) by island but with Corsican populations split into two groups as suggested by the phylogeographic and NCPA results. We also used ARLEQUIN to calculate pairwise F_{ST} values for all pairs of populations; statistical significance of F_{ST} values was assessed by 1,000 permutations with sequential Bonferroni correction for multiple tests.

RESULTS

Sequence Variation

We sequenced 1,143 bp of mtDNA (675 bp for the COI gene and 468 bp for the 16S rRNA gene) for each individual included in the study. We observed only few gaps in the final alignment all in the 16S gene and confined to outgroup vs. ingroup comparisons. Levels of sequence variability were slightly higher in COI than in 16S; there were 50 (7.40%) polymorphic sites in COI and 33 (7.05%) in 16S; parsimony informative sites were 35 (5.18%) and 10 (2.13%) for the two genes. As expected, most of the variation resided in COI 3rd codon positions; 43 (19.11%) sites were variable, and of these 31 (13.7%) were also parsimony informative. The combined data set had 83 (7.26%) and 45 (3.93%) variable and parsimony informative sites. Sequences were generally A+T rich and anti-G biased, a typical pattern for mitochondrial genomes. A+T percentages ranged from 57.5% in COI 1st codon positions to 88.9% in COI 3rd codon positions; G percentages varied from 5.3% in COI 3rd codon positions to 27.9% in COI 1st codon positions. A χ^2 test of homogeneity of base frequencies among taxa did not reveal any significant differences, irrespective of the data partition tested (both genes combined,

TABLE 2. Haplotype frequencies of all individuals of *Solatopupa guidoni* sequenced for the study. For population codes see Fig. 1. Numbers in brackets are sample sizes.

Haplotype	Populations								
	Sardinia			Corsica				Elba Is.	
	CCC (3)	COR (16)	SBR (4)	FRA (3)	CAP (5)	OLE (9)	FLO (10)	SIS (8)	GRO (2)
1					1				
2					1				
3					1				
4					1				
5					1				
6	3								
7		14							
8		1							
9		1							
10							8		
11							1		
12							1		
13				3					
14									2
15						8			
16						1			
17			4						
18								1	
19								4	
20								2	
21								1	

each gene separately and COI 1st, 2nd, and 3rd codon positions separately). Visual inspection of saturation plots (not shown) revealed that saturation is not present in the data set.

Haplotype Frequencies and Genetic Variability of Populations

The 60 sequences yielded 21 haplotypes (Table 2). These were population-specific (i.e., not shared among populations) and differed by 1 to 23 substitutions. COR, CAP, OLE, FLO and SIS had more than one haplotype with a maximum number of five in CAP (Table 2). CCC, SBR, FRA and GRO were fixed for single haplotypes. In the other populations, haplotype diversity (*h*) ranged between 0.222 ± 0.166 (OLE) and 1.000 ± 0.126 (CAP); the mean number of pairwise differences between all pairs of haplotypes (π) and nucleotide diversity (π_n)

was lowest in COR (0.375 ± 0.376 and 0.0003 ± 0.0003) and highest in OLE (4.666 ± 2.523 and 0.004 ± 0.002).

Phylogenetic Analyses and Divergence Times

Figure 2 shows the haplotype Bayesian tree obtained for the combined data set using the GTR + I model (proportion of invariable sites = 0.876, equal distribution of rates at variable sites) and summarizes the results of the NJ searches. Both trees were statistically indistinguishable with the AU test (*P* = 0.641) and identified two major haplotype groups. A first group received good bootstrap support (89%) but fair posterior probability (89%); this group included haplotypes from Sardinia, Corsica, and Elba Island. Relationships within this clade were generally supported. Haplotypes from two Corsican localities (FLO and OLE) did not form

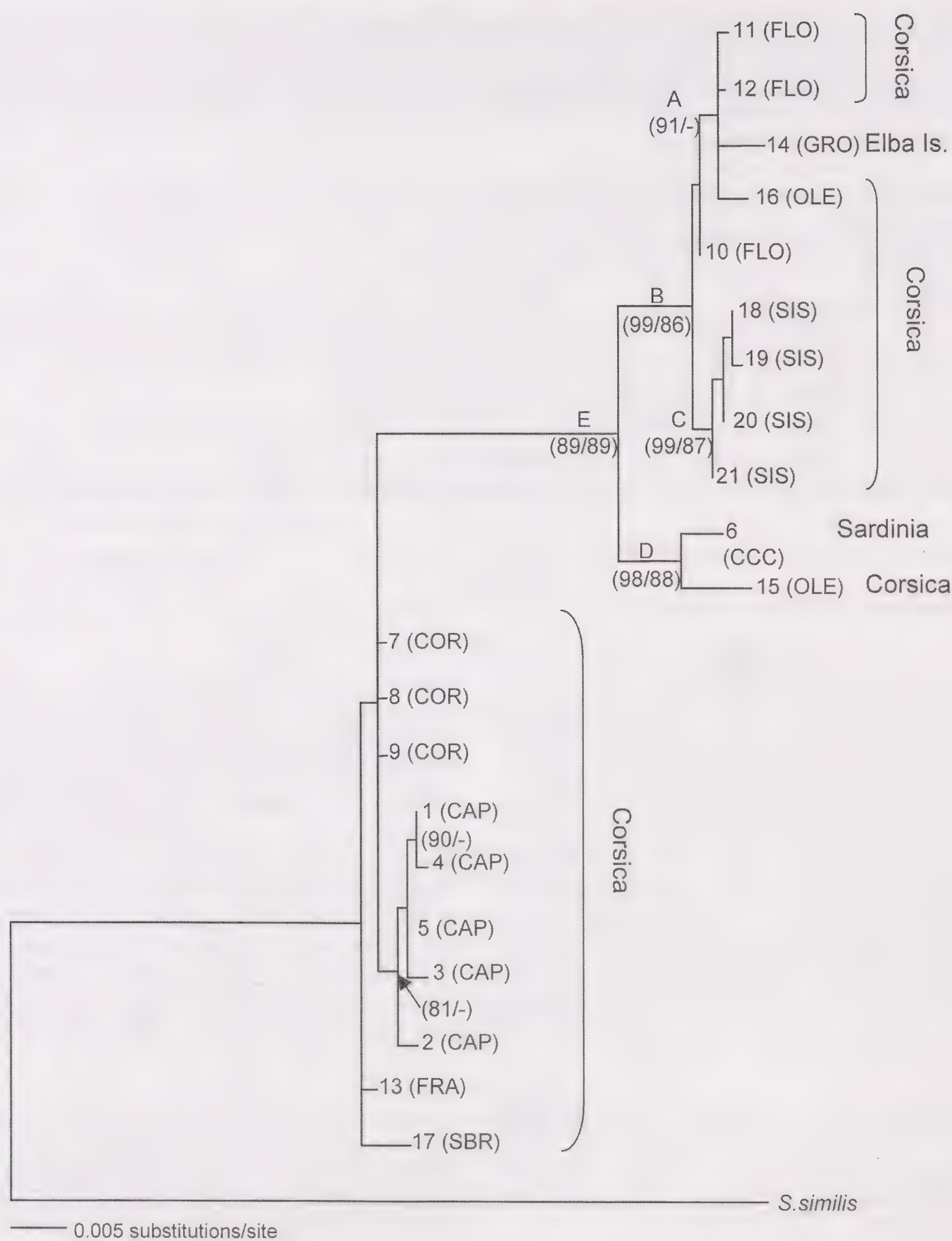


FIG. 2. Bayesian haplotype phylogram based on the GTR+I model of sequence evolution. Only statistical supports $\geq 75\%$ for both the Bayesian (2,000,000 generations) and NJ searches (1000 bootstrap replicates) are reported on branches (first and second values). Population codes are as in Table 1 while haplotype numbers are as in Table 2. A, B, C, D and E identify nodes for which estimates of divergence times have been calculated (Table 3).

monophyletic clusters. Rather, haplotype 10 (FLO) grouped with one of the two haplotypes found at OLE (16) plus the haplotype sampled on Elba Island (GRO). The second haplotype from OLE (15) was sister to haplotype 6 found

on Sardinia. The second group only included Corsican haplotypes. Relationships within this clade were poorly resolved, with only a low support (81%) for haplotypes from CAP as monophyletic in the Bayesian analysis.

TABLE 3. Inferred divergence times (Myr) based on the COI and 16S data partitions and on a variety of published rates for mollusks for supported splits in the *Solatopupa guidoni* haplotype tree of Fig. 2 (nodes A-E). Maximum Likelihood distances (D_{ML}) are based on the models of sequence evolution that best fitted the two data partitions (models selected with MODELTEST). *Rates from Ozawa & Okamoto, 1993; Rumbak et al., 1994; and Marko, 2002. **Substitution models are GTR + I and F81 for COI and 16S data partitions, respectively.

Data partitions/ Rates* (%/Myr)		COI 0.67–1.08		16S 0.5–0.6	
Node	D_{ML} **	Myr		D_{ML} **	Myr
A	0.007 ± 0.002	0.52 ± 0.14	0.32 ± 0.009	0.0005 ± 0.0005	0.05 ± 0.05 – 0.04 ± 0.04
B	0.01 ± 0.001	0.75 ± 0.07	0.46 ± 0.046	0.0012 ± 0.001	0.12 ± 0.100 – 0.1 ± 0.083
C	0.001 ± 0.0006	0.07 ± 0.044	0.05 ± 0.027	0.000	-
D	0.015	1.12–0.69		0.009	0.9–0.75
E	0.034 ± 0.001	2.53 ± 0.07	1.57 ± 0.046	0.004 ± 0.0004	0.4 ± 0.03 – 0.33 ± 0.03

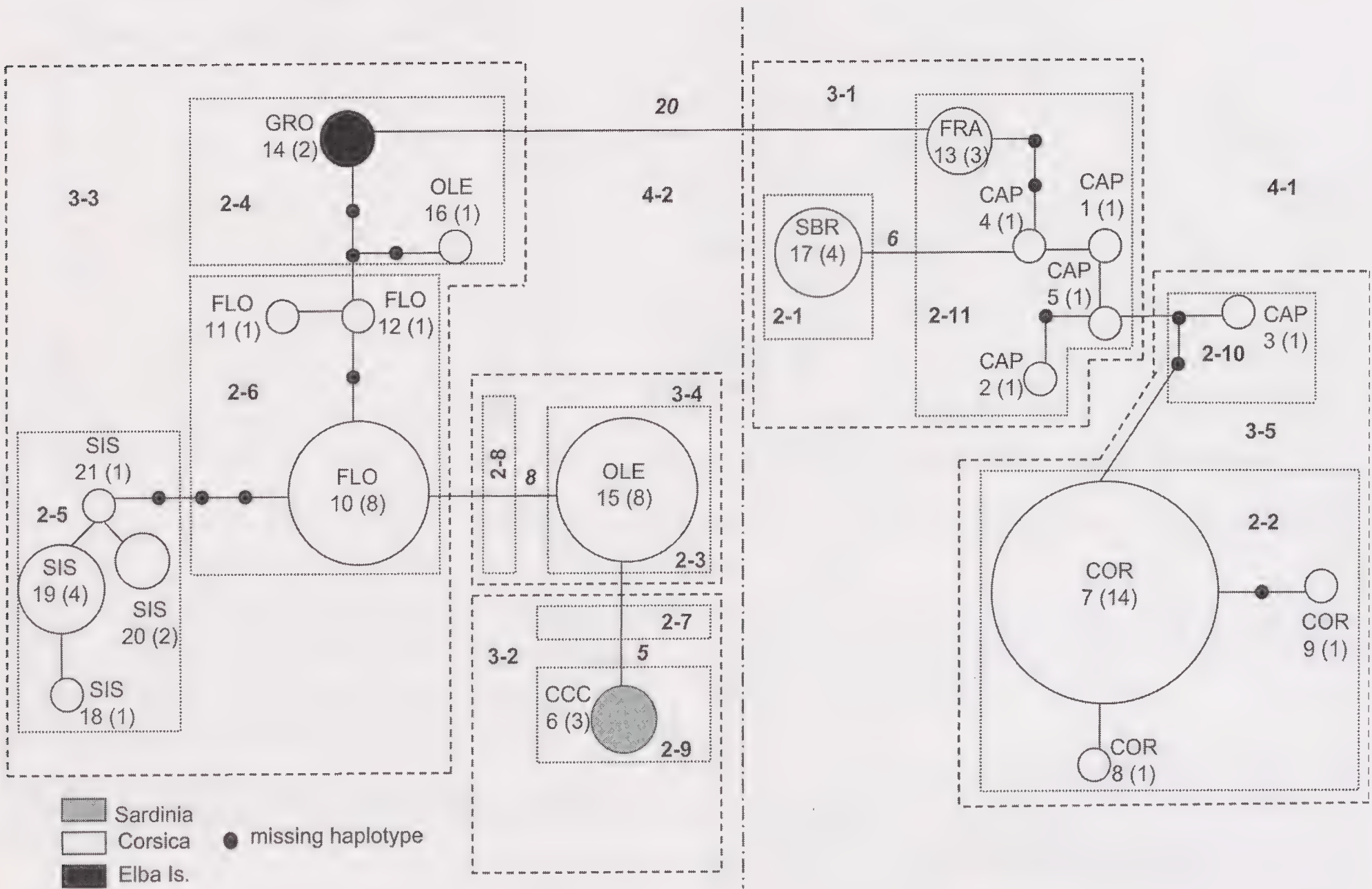


FIG. 3. Haplotype network and Nested Clade Phylogeographical Analysis of *Solatopupa guidoni* populations derived from COI + 16S data. The relative size of the circles is proportional to the number of individuals carrying that particular haplotype; different shadings indicate the geographic origin of haplotypes. Coding of populations and numbering of haplotypes are as in Tables 1 and 2. Numbers in parentheses indicate how many individuals carried that particular haplotype. Black dots are missing haplotype. Haplotypes are always one mutational step away from each other if not indicated otherwise (i.e. when the number of steps was higher than 4 numbers in italics are the mutational steps necessary to connect haplotypes; missing haplotypes are not represented in these particular circumstances). The Figure also shows the nesting design as obtained with ANeCA. Clades are designed as x-y, where x represents the nesting level (from the haplotype to the 4th level but haplotype and 1-step levels are not shown) and y is the number assigned to that particular clade.

TABLE 4. Nested clade analysis of the geographical distribution of *Solatopupa guidoni* haplotypes. Only the six clades with significant GEODIS results are shown (see *P* value of the χ^2 test; third column). Clade names and nesting design are as in Fig. 3; the geographical distribution of clades is also shown. The last two columns show the sequence followed in the inference key implemented in ANeCA and the resulting biological inference.

Clade	Distribution	<i>P</i>	Inference key sequence	Biological inference
2-11	FRA, CAP (Corsica)	0.050	1,2, tip-interior status cannot be determined	Inconclusive outcome
3-1	SBR, FRA, CAP (Corsica)	0.005	1,19, no	Allopatric fragmentation
3-3	OLE, FLO, SIS, GRO (Corsica, Elba Is.)	0.000	1,2,11,12, no	Contiguous range expansion
4-1	COR, SBR, FRA, CAP (Corsica)	0.000	1,2, tip-interior status cannot be determined	Inconclusive outcome
4-2	CCC, OLE, FLO, SIS, GRO (Sardinia, Corsica, Elba Is.)	0.000	1,2,3,4,9, no	Allopatric fragmentation
Total	All populations (Sardinia, Corsica, Elba Is.)	0.000	1,2, tip-interior status cannot be determined	Inconclusive outcome

Because the Corsican populations did not form a monophyletic group, we tested this alternative hypothesis against the unconstrained topology presented in Figure 2. Yet, the AU test rejected the monophyly of the Corsican populations (*P* = 0.008).

The LRT test conducted on trees with and without the molecular clock alternatively relaxed and enforced could not reject the hypothesis of homogeneous rates along the branches of our phylogeny [-lnLnoclock = 2114.27; -lnLclock = 2115.13; 2Δ*L* = 1.72; degrees of freedom = 20; critical χ^2 value (*P* = 0.05) for 20 degrees of

freedom = 31.41]. We could therefore calculate divergence times for labeled nodes in the tree of Figure 2 (A to E); the results of these calculations are presented in Table 3. These estimates have to be considered cautiously, as not all the above nodes were unambiguously supported by our phylogenetic searches though the network analysis retrieved almost identical groupings. Time estimates based on COI ranged in age from 0.05 ± 0.027 Myr (node C) to 2.53 ± 0.07 Myr (node E); those based on 16S varied between 0.04 ± 0.04 Myr (node A) and 0.4 ± 0.03 Myr (node E).

TABLE 5. Results from the analysis of molecular variance (AMOVA). Populations have been grouped alternatively into three (scheme I) or four groups (scheme II). Scheme I corresponds to the three islands (Sardinia, Corsica and Elba Island) sampled for the study while in scheme II we split Corsican haplotypes into two groups (COR, SBR, FRA, CAP and OLE, FLO, SIS, respectively), as suggested by phylogenetic and network analyses (Figs. 2, 3).

Analysis structure	Source of variation	Sum of squares (d.f.)	Variance component	<i>P</i>	Fixation index	% of variation
Scheme I	Among groups	2.68 (2)	Va = 0.062	0.040	Φ _{CT} = 0.113	11.35
	Among populations	15.01 (6)	Vb = 0.310	0.000	Φ _{SC} = 0.636	56.44
	Within populations	9.02 (51)	Vc = 0.180	0.000	Φ _{ST} = 0.677	32.21
Scheme II	Among groups	6.12 (3)	Va = 0.023	0.000	Φ _{CT} = 0.047	8.94
	Among populations	11.56 (5)	Vb = 0.305	0.000	Φ _{SC} = 0.633	63.32
	Within populations	9.02 (51)	Vc = 0.176	0.000	Φ _{ST} = 0.650	27.74

TABLE 6. F_{ST} values among the *Solatopupa guidoni* populations included in the study. Bold numbers indicate statistical significance after sequential Bonferroni correction for multiple comparisons (significance assessed by 1,000 permutations in ARLEQUIN 3.01).

	Sardinia				Corsica			Elba Is.	
Population	1	2	3	4	5	6	7	8	9
1-CCC	-								
2-COR	0.798	-							
3-SBR	1.000	0.809	-						
4-FRA	1.000	0.798	1.000	-					
5-CAP	0.387	0.519	0.452	0.387	-				
6-OLE	0.828	0.765	0.843	0.828	0.469	-			
7-FLO	0.711	0.703	0.733	0.711	0.377	0.696	-		
8-SIS	0.479	0.563	0.522	0.479	0.138	0.524	0.449	-	
9-GRO	1.000	0.784	1.000	1.000	0.285	0.809	0.681	0.415	-

Nested Clade Phylogeographical Analysis, AMOVA and F_{ST} values

Figure 3 illustrates the network obtained with TCS (Clement et al., 2000) and shows the nesting design with four nested levels. The

pattern of relationships in the network was generally congruent with that depicted by the phylogenetic tree of Figure 2. Clades 4-1 and 4-2 corresponded to the two major groups of haplotypes found in the phylogenetic searches. These clades were separated by a deep phy-

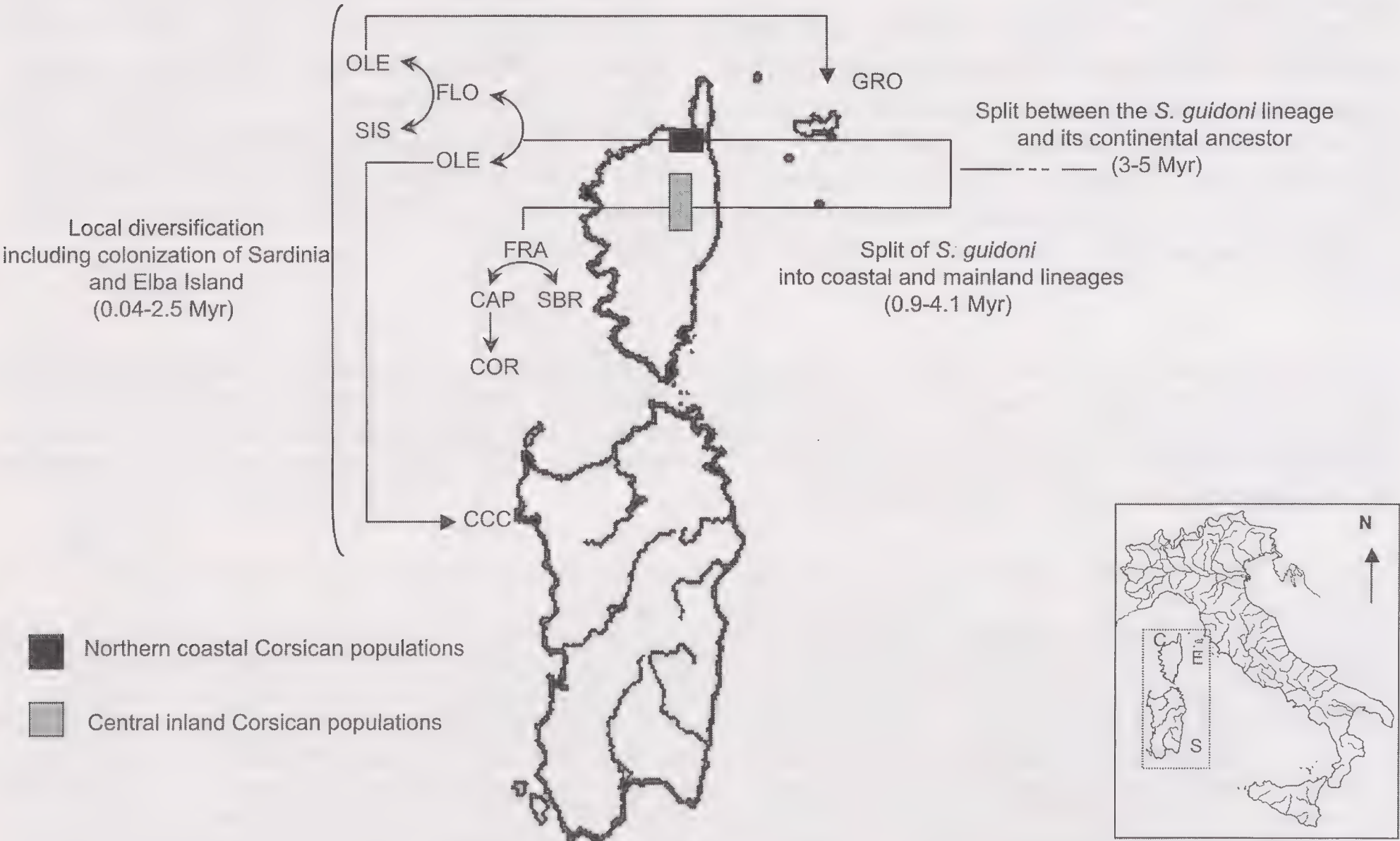


FIG. 4. Schematic of proposed phylogeographic history of *Solatopupa guidoni* with patterns and timing of the major events of differentiation within the species as inferred from phylogenetic and nested clade analyses combined with molecular clock estimates. See text for detailed discussion.

logeographic break of 20 substitutions. The two haplotypes from OLE (15 and 16) were not linked to each other. Overall, the network analysis confirmed that the Corsican haplotypes do not form a monophyletic entity and can be split into two major sub-groups. The nesting procedure produced eight clades that could be tested for geographical association, and six of them resulted in significant permutational contingency tests indicating a non-random geographical distribution of haplotypes (Table 4). The inferences derived from Templeton's keys suggested allopatric fragmentation for clades 3-1 and 4-2 and contiguous range expansion for clade 3-3. In three circumstances (2-11, 4-1, and for the total cladogram) the inference keys gave inconclusive outcomes because of the unresolved status of tip-interior position of the clades.

Hierarchical analysis of molecular variance (AMOVA) is reported in Table 5. Pooling Corsican populations in a single group or splitting them into two groups did not change the main outcomes of the analysis. AMOVA showed that most genetic heterogeneity was apportioned among populations within groups and within populations. Together these two levels explain between 87% and 92% of the overall variation, depending on the hierarchical scheme adopted (I or II; Table 5). These results, along with those of the pairwise F_{ST} analysis reported in Table 6, indicate a general high level of genetic differentiation. The vast majority of pairwise F_{ST} values were over 40% and statistically significant after sequential Bonferroni correction.

DISCUSSION

The main findings of this study can be summarized as follows: *S. guidoni* is a genetically structured species that can be broadly divided into two lineages. One of these lineages is limited to central inland Corsica, while the second includes northern coastal Corsica sites plus Sardinia and Elba populations. Patterns of relationships suggest that differentiation within Corsica predated between-island divergence. This translates into a lack of reciprocal monophyly of lineages occurring on the three land-masses. While Sardinia and Elba both harbor monophyletic (monotypic) lineages (but a very limited number of individuals were analyzed for these locations), they are nested in one of the Corsican clades.

Levels of Divergence and Population Structure

Numerous studies have revealed a broad range of intraspecific mtDNA differentiation in terrestrial mollusks (2.9–30% of sequence divergence) (Thomaz et al., 1996; Pfenninger & Magnin, 2001; Davison, 2002; Holland & Hadfield, 2002; Uit de Weerd et al., 2005). We found an average level of sequence divergence of $3.6 \pm 0.2\%$ between the two alleged haplo-groups of *S. guidoni*. This is close to the lower bound of the aforementioned range of mtDNA variation. These results suggest that processes of differentiation within the species are relatively recent. Our molecular clock estimates below support this hypothesis. In addition, Giusti (1977) stressed that there are no clear differences in shell morphology or internal anatomy that could help distinguish Sardinian, Corsican, and Elba Island populations from one another. Thus, neither genetics nor morphology (Giusti, 1977) support the need for taxonomic revision of the species, contrary to the claim of Boato et al. (1985).

On the other hand, our data indicate a general lack of gene flow among populations of *S. guidoni*, as attested by haplotype frequencies, AMOVA results and generally high and significant pairwise F_{ST} values. AMOVA showed that populations were significantly differentiated at all three levels of the hierarchical design, with a large fraction of variation apportioned among populations, whatever hierarchical scheme was adopted in the analysis (Table 5). These results are in line with allozyme data that demonstrated a substantial lack of gene flow in the species, with populations bearing a considerable number of private and fixed alternative alleles and with an average number of migrants per generation among locations of 0.036 (Boato, 1988). Concordant patterns in markers with different characteristics (nuclear vs. mitochondrial) suggest the same underlying evolutionary scenario. These results also fit well with some general characteristics of land snails. Populations of these organisms are often divided into small breeding units (demes) that are partially, if not completely, isolated from one another by habitat discontinuities. Movements of individuals between demes are very rare, since distance between nearby demes is usually larger than the average dispersal range of individuals (Fiorentino et al., 2009, and references therein). It is therefore not surprising that most of the molecular papers

published so far on terrestrial mollusks have revealed considerable population structuring and geographic variation (reviewed in Davison, 2002). Stochastic processes (i.e., genetic drift and founder effect) have been identified as the prominent factors shaping genetic traits of populations. Coalescence of haplotypes is another process that might account for population division in terrestrial mollusks. Their populations are typically arranged in a stepping-stone fashion and divided into discrete demes of large size (hundreds or thousands of individuals). Their high density and the limited migration of individuals between them theoretically translate into much longer persistence (time to common ancestor) of mitochondrial haplotypes with retention of ancient lineages and thus into an increase in overall divergence (Thomaz et al., 1996). It must be noted, however, that population size in *Solatopupa* tends to be small compared to that of other snails and occurrence of demes is scattered (Boato, 1988). These seem to be common traits in rock-dwelling species bound to calcareous substrata (Fiorentino et al., 2009). Moreover, rocks of different geological nature surround the limestone occupied by the species constituting a major impediment to dispersal. Assuming, contrary to what is commonly reported for other land snails, that *S. guidoni* populations are arranged in scattered demes of small size, we argue that time to coalescence may be relatively short, explaining the rather shallow level of divergence.

Historical Biogeography

A number of molecular studies on a taxonomically diverse array of organisms endemic to the peri-Tyrrhenian area have been carried out in the last decade. The organisms include newts, subterranean terrestrial and aquatic isopods, stoneflies, and flightless beetles (Cobolli Sbordoni et al., 1995; Caccone et al., 1997; Ketmaier et al., 1999, 2000, 2003a, b; Fochetti et al., 2004). All these organisms are found in Sardinia and Corsica and some of them also occur in the Tuscan archipelago or coastal areas of Tuscany, that is, the terrestrial and aquatic isopod genera *Oritoniscus* and *Stenasellus* (Cobolli Sbordoni et al., 1995; Ketmaier et al., 1999, 2000, 2003a). In all circumstances, phylogenetic analyses were concordant in sorting Sardinian and Corsican taxa into distinct groups separated by large mutational distances. Tuscan representatives,

if any, were always more closely related to the Corsican than to the Sardinian taxa (Cobolli Sbordoni et al., 1995; Ketmaier et al., 1999, 2000, 2003a). Interestingly, a major phylogeographic break between Corsica and Sardinia and a closer affinity between populations from Corsica and the Tuscan archipelago has also been found in plants belonging to the genus *Borago* (Selvi et al., 2006). Conversely, we did not find reciprocally monophyletic lineages in *S. guidoni* on the three islands.

Given the lack of fossil evidence for *S. guidoni*, which prevents the use of tree-based estimates of time divergences (Sanderson, 1997, 2002, 2003), we could only rely on rates published for mollusks. It is important to stress that mtDNA substitution rates are a notoriously difficult issue in gastropods because of their extensively documented accelerated rates of evolution (Chiba, 1999; Pinceel et al., 2005). However, we tend to reject this hypothesis for *S. guidoni* on the grounds of the available allozyme data (Boato, 1988). MtDNA and allozymes support concordant patterns of relationships as shown here. According to Pinceel et al. (2005), this is good evidence that mt- and nuclear DNA rates are not strongly decoupled with mtDNA evolving much faster than nucDNA. If they were, we would have observed divergence in the mtDNA but sharing of alleles at the allozyme loci across locations, which is not the case here as different populations are characterized by a high percentage of private alleles (12.5%; Boato, 1988). Additionally, time estimates for the statistically supported nodes in our phylogeny are all relatively recent, not older than 2.5 Myr. While these are only crude estimates of minimum time since divergence and are based on a not fully supported phylogeny, they are in line with the time frame of genus cladogenesis, which took place between the middle Miocene and the middle-late Pliocene (Ketmaier et al., 2006).

Previous allozyme and DNA sequence data had already suggested that Corsican populations might be divided into a central inland and a northern coastal clade (Boato, 1988; Ketmaier et al., 2006). These would correspond to clades 4-1 and 4-2 of our study (Fig. 3). Sardinian and Elba Island haplotypes are linked to the northern coastal clade. Boato (1988) found a sister relationship between a population sampled close to OLE (Col de Teghine, black dot in Fig. 1) and CCC (same locality as in the present study), but no samples from Elba Island were included in that study. In our previous paper,

we retrieved a sister relationship between CCC and GRO, but only analyzed two mainland Corsican populations (FRA and SBR) (Ketmaier et al., 2006). The occurrence of the species on Sardinia and Elba Island can be explained in the light of the paleogeographic history of these landmasses and their connections to Corsica. According to Steininger & Rögl (1984), Corsica and Sardinia became permanently isolated in the Pliocene (5 to 3 Myr BP). More recent data, however, suggests that this is an over-simplified scenario and that multiple relatively short-lived connections between the two islands existed during the Quaternary, up to 20,000 years ago at each glacial peak, as a consequence of the worldwide drop in sea level (Meulenkamp & Sissingh, 2003; Pascucci, per.com.). Our time estimates for the split between the Sardinian population and its closest Corsican relative (haplotype 15, OLE) range from 0.7 to 1.12 Myr BP, depending on the gene used and the substitution rate adopted (Table 3). Although these datings span a relatively broad time scale, they overlap remarkably with the Günz glaciation (West, 1977). They suggest that a (possibly single) dispersal event of the species from Corsica to Sardinia took place at that time, but not during more recent Quaternary connections between the two islands. This hypothesis is further supported by the fact that in Sardinia the species is limited to two nearby locations (Fig. 1), despite the extensive occurrence of limestone throughout the island. The haplotype sampled on Elba Island is deeply embedded within Corsican haplotypes in the phylogenetic tree (Fig. 2), while it has a tip position in the haplotype network (Fig. 3). According to our time estimates, differentiation within this haplogroup occurred in the Pleistocene, between 0.04 and 0.52 Myr BP. Anti-clockwise rotation of the Sardinia-Corsica microplate caused uplifting of coastal Tuscany, including the Tuscan archipelago, which has been repeatedly connected to Corsica as well as to coastal Tuscany during the Quaternary (Lipparini, 1976; Cherchi & Montadert, 1982; Burgassi et al., 1983; Pascucci et al., 1999). As a consequence, the archipelago hosts a fauna transitional between the two areas. The incidence of continental Tuscan and Corsican species in the Tuscan archipelago is directly related to the present-day distance of the different islands from the two source areas, with Elba Island playing the role of stepping stone (Dapporto et al., 2007, and references therein). A close phyletic relationship between Corsican and insular Tuscan

species has frequently been found for species with poor dispersal capacities, such as stygobiont taxa (Ketmaier et al., 2003a). This led to the recognition of a Corsica-Sardinian stygofaunal province that also includes the insular areas of Tuscany (Pesce, 1985). We conclude that the most parsimonious scenario to account for the exclusive occurrence of the species on Elba Island (and not on any other island of the Tuscan Archipelago) is based on dispersal. Our time estimate for this event suggests that the species reached Elba Island more recently than Sardinia.

The Phylogeographic Scenario

The nested clade analysis suggests a dispersal event between Corsica and Elba Island with contiguous range expansion (clade 3-3; Fig. 3). This implies movements of individuals as connections between landmasses became available. For clades 3-1 (central inland Corsican lineage) and 4-2 (Sardinia, coastal northern Corsica and Elba Island), the analysis indicated allopatric fragmentation as the most likely biological inference. A combination of vicariance and dispersal events would therefore most effectively explain the current distribution of the species. Phylogeographic relationships within *S. guidoni* are evidently complex; Figure 4 summarizes the following discussion. Based on our phylogenetic, nested clade and molecular clock analyses we propose that immediately after the split from its continental sister taxon, *S. guidoni* underwent further division into a coastal northern and central inland Corsican lineage. Diversification within the latter group is presumably allopatric and associated with the scattered distribution of suitable calcareous rocks among geologically different substrata. Relationships within the coastal lineage are less clear. A first split separated FLO from OLE (haplotype 15, the most abundant in the latter population). The occurrence of the species in Sardinia is difficult to explain because of the large geographical gap separating the Sardinian population from its closest extant population (OLE). In addition, *S. guidoni* has never been found in southern Corsica, despite extensive surveys in the only area with limestone (Bonifacio; shaded in grey in Fig. 1). We cannot exclude that *S. guidoni* had a broader range, occurred there sometime in the past and then became extinct; unfortunately, this is a hypothesis that currently cannot be tested. According to the haplotype network (Fig. 3),

FLO gave rise to SIS, probably through a single founder event, as supported by the monophyly of SIS (Figs. 2, 3). Nearly coeval with this was the origin of the lineage that includes the second haplotype found at OLE (haplotype 16) and the haplotype found on Elba Island. The occurrence of divergent haplotypes at OLE implies admixture between presumably allopatrically evolved haplotypes (Avise, 2000). The only known population in the area that we were not able to sample is Col de Teghine (Fig. 1). This population (but not OLE) was included in the allozymic survey of Boato (1988) and it showed affinity with FLO, while bearing private alleles. We tentatively conclude that at OLE a more divergent haplotype (15) met haplotype 16 of more recent origin.

This study reveals that within-island divergence in *S. guidoni* is slightly older than between-island differentiation and that Corsica (the most intensively sampled island) does not harbor a monophyletic lineage. While very little can be derived for Sardinia and Elba Island because of the small sample sizes, for Corsica our results do not support a one island-one clade association, even in an organism with theoretical poor dispersal capacity and distributed over biogeographically well-known areas.

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BRACHIOPOD IDENTITY OF THE ALLEGED MONOPLACOPHORAN ANCESTORS OF CEPHALOPODS

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ABSTRACT

Because of a serial arrangement of supposed pedal muscles and its high-conical shell, *Hypseloconus* from the Late Cambrian to Early Ordovician of North America is generally believed to be a monoplacophoran relative of cephalopods. The distinctive pattern of muscle attachments and shell form indicates its close relationship to roughly coeval Siberian *Kirengella* and several other genera classified in the order Kirengellida. Newly collected material from the Early Ordovician of Siberia shows that the bivalved *Angarella*, with its ventral valve cementing to a hard substratum, is closely similar to *Kirengella* and *Hypseloconus* in the arrangement of shell muscles. Permanently fixed to its substratum was also another probable member of the group, *Pygmaeoconus*. Musculature of *Angarella* in some aspects resembles that of the Early Cambrian mobergellans with phosphatic shells, but in the calcitic shell structure it is similar to the craniopsid brachiopods. Irrespective of whether the kirengellids are brachiopods or not, they should be removed from considerations on the ancestry of cephalopods. The alternative to *Hypseloconus* as a candidate for cephalopod ancestry is the Early Cambrian *Turcutheca*, an enigmatic mollusk with endogastrically curved and laterally compressed conch and relatively large subspherical embryonic conch, in both aspects resembling the earliest ellesmeroceratid nautiloids.

Key words: Monoplacophora, Ordovician, Cephalopoda, Siberia, evolution.

INTRODUCTION

Embryological and comparative anatomical evidence is widely used to interpret the origin of aspects of cephalopod soft anatomy distinctive for them, whereas palaeontological data show how their shell, of originally hydrostatic function, changed in the course of evolution. The most widely accepted palaeontological interpretation of the origin of cephalopods, advanced by Yochelson et al. (1973) and reaffirmed in Webers & Yochelson (1989) and Kröger (2007), proposes that they originated from a high-conical monoplacophoran with serially arranged pedal muscles. The only available evidence that such monoplacophorans occurred in the Cambrian, before the appearance of earliest cephalopods, are specimens of *Hypseloconus* cf. *H. stabilis* Berkey, 1898, from the Davis Formation of Missouri described by Stinchcomb (1980). Webers et al. (1991) and Stinchcomb & Angeli (2002) transferred this species to the roughly coeval Siberian genus *Kirengella*, which shows a similar disposition of muscle attachments

on the shell interior. *Kirengella* differs from *Hypseloconus* in having a low-conical shell. As shown below, an even lower shell, but virtually the same pattern of muscle attachment scars, characterizes *Angarella*, fossil shells of which abundantly occur in the Ordovician strata of the region. But at this point of reasoning a great difficulty emerges: *Angarella* shells are bivalved and were basally cemented to a hard substratum! These extinct organisms appear to be more similar to the craniopsid brachiopods than to the monoplacophorans.

In the present paper I present data on the morphology of *Angarella* and discuss its evolutionary relationships with coeval brachiopods and possibly ancestral Cambrian problematica. An alternative direction of search for cephalopod ancestry will be proposed.

MATERIAL

Angarella shells are the most common fossils in the Badaranovo Formation of the Irkutsk

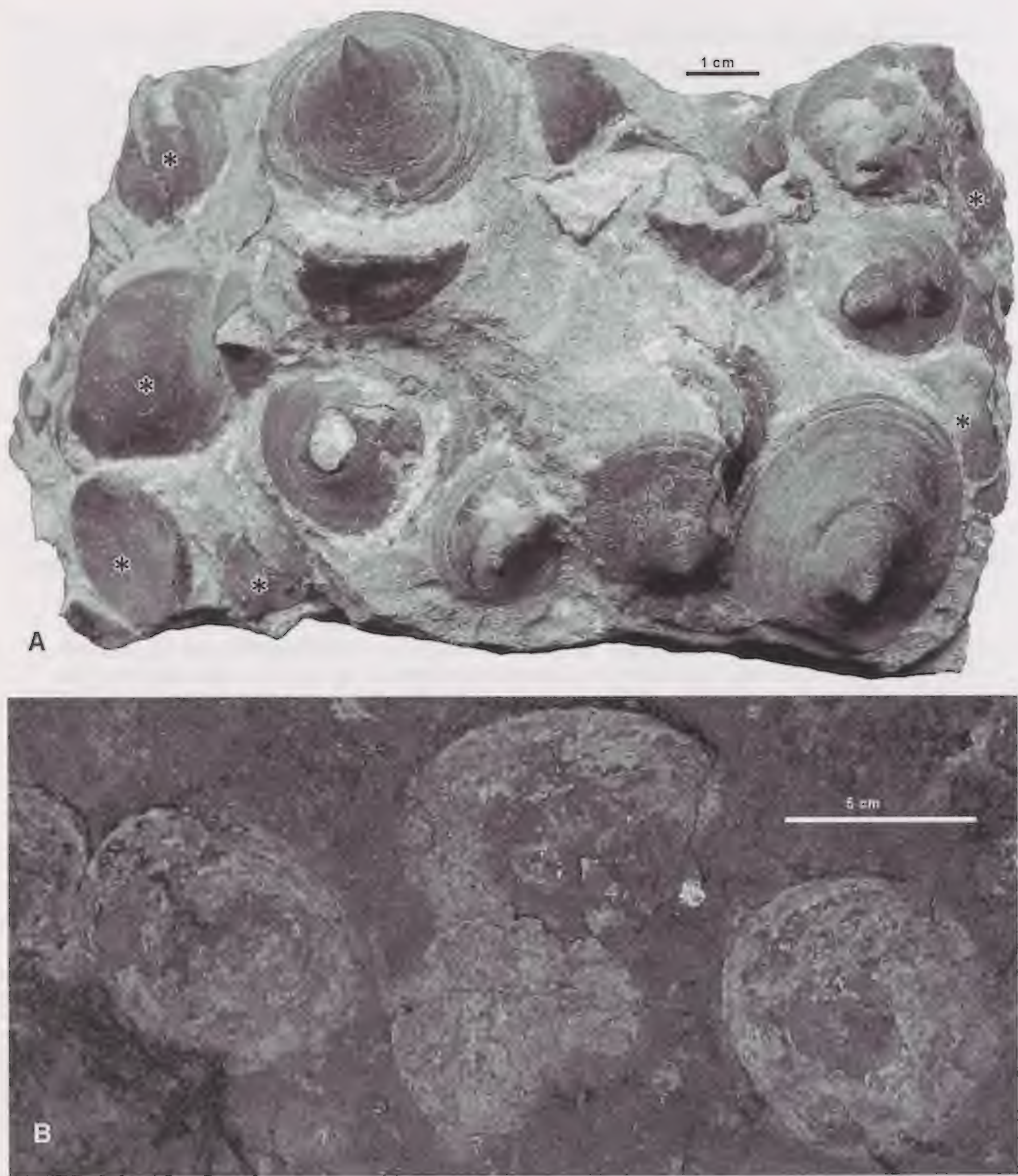


FIG. 1. Species of *Angarella* from the Ordovician of the Angara River region, Siberia. A: Mass occurrence of *Angarella jaworowskii* Asatkin, 1932, shells in light coarse-grained calcareous sandstone of the lower Badaranovo Formation; loose block ZPAL Bp 62/12 collected at Pashino near Kodinsk. Ventral valves are marked with asterisks; B: Large ventral valves of *Angarella* at the bedding surface of red muddy calcareous sandstone of the lower Mamyry Formation at the bank of Vikhoreva River near Bratsk (field photo).

Amphitheatre geological structure in southern Siberia (Divina et al., 1984). Frequently they are rock-forming skeletal elements. Their preservation is generally poor, and morphological details

of the shell surface or interior are rarely discernible. The specimens used in this study come from a loose block of calcareous sandstone collected on the left bank of Angara near Ko-



FIG. 2. Morphology of *Angarella jaworowskii* Asatkin, 1932. Shells from a loose block of sandstone of the lower Badaranovo Formation collected at the bank of Angara at Pashino near Kodinsk, Siberia. A–C: Dorsal valve ZPAL Bp 62/6 with muscle attachment scars, lateral and external views of part (A–B) and internal view of counterpart (C); D: Ventral valve ZPAL Bp 62/8 in internal view; E: Same for ventral valve ZPAL Bp 62/7; F–G: Lateral and external view of extremely high-conical dorsal valve ZPAL Bp 62/25 with thin wall; H–I: Same views of small-conical dorsal valve ZPAL Bp 62/27 with thick wall.

dinsk upstream of Verkhnyaya Kezhma Creek, where formerly the village Pashino was located. The material is relatively informative owing to weathering of the rock, which then easily disintegrates along the shell surfaces. The block probably derived from the 1.5 m thick bed 43 of the Badaranovo Formation, where a mass occurrence of *Angarella* was reported by Kniazev (1978). There was little sorting, as ventral and dorsal valves seem to be equally frequent in the rock (Figs. 1A, 2). The fossil assemblage in the block is monospecific, but in other beds of the formation *Angarella* is sometimes associated with sinuitid bellerophonts.

This material of *Angarella* Asatkin, 1932, almost certainly represents the type species of the genus, *A. jaworowskii* Asatkin, 1932, and derives from its type stratum, the Badaranovo Formation. The type locality is within the same region on Angara at the mouth of the Koda River. Each sample of *Angarella* shells from the Badaranovo Formation shows so much variability in the shape of both ventral and dorsal valves that discrimination seems hardly possible. Originally four species of the genus were named, and Yadrenkina (1984) reduced their number to three, but all occur together in various horizons of the formation.

In relatively pure reddish sandstone of the lower Badaranovo Formation on Angara, specimens with marginal concentration of growth increments are mostly of 3 cm diameter and rarely approach 4 cm. Specimens possibly representing a more advanced segment of the *Angarella* lineage or a local population living in a different environment occur in olive-gray marly sandstone of the upper Badaranovo Formation exposed near Kodinsk a few kilometers upstream from the place where specimens with muscle scars were collected (near the former village Rozhkovka). The stratum probably represents the basal horizon in the upper Badaranovo Formation. Specimens of *Angarella* reach there oyster size, up to 12 cm long (Fig. 3B). At Rozhkovka the large *Angarella* is a member of a rather diverse fossil assemblage with conodonts, suggestive of an open-sea environment with normal salinity. Similar, but usually poorly preserved specimens of *Angarella* occur in the cliff of Vikhoreva River, a tributary of Angara near Bratsk (Fig. 1B). The stratigraphically highest occurrence of *Angarella* at Vikhoreva is in the marly oolitic limestone of the lower Mamyry Formation in an abandoned quarry on the other side of the road (exposure 755 in Divina et al., 1984). Large *Angarella* are associated with the raphistomatic gastropods and

bellerophonts indicative of more open marine conditions than lower in the section.

Specimens are housed at the Institute of Paleobiology of the Polish Academy of Sciences in Warszawa, Poland (ZPAL).

GEOLOGICAL AGE OF THE FAUNA

In the Ordovician, the Siberian Platform was a separate continent with faunas biogeographically distinct from those of other regions of the world. Only some species of pelagic organisms had their distribution wide enough to enable age correlation. In the Angara section, the conodonts may serve this purpose, but our knowledge about them is at a rather preliminary stage, with the standard apparatus-based taxonomy applied to only a few species, none from the Badaranovo Formation. A brief overview of the evidence thus seems necessary.

Conodont samples rich enough to enable the apparatus study have been obtained from two glauconitic limestone beds near the base of the formation. They are underlain by mudstone beds, and overlain by reddish sandstone, with the *Angarella*-rich horizon a few meters higher. Glauconite is the main component of the rock in the basal bed of the Badaranovo Formation (Ang-3), whereas quartz sand dominates in the bed 40 cm higher in the section (Ang-2). Conodont faunas from these beds are closely similar to each other.

The most common conodont is a species of *Drepanoistodus* (141 specimens in Ang-3; 122 in Ang-2) with rather robust elements lacking any additional ribs (Moskalenko, 1984). Some elements resemble *Drepanodus* and were classified as such by Moskalenko (1984), but no symmetrical S_0 or geniculate M elements in the samples represent this genus. The second in number (19 specimens in Ang-3; 30 in Ang-2) is a similarly generalized species of *Acodus* with minute elements (possibly *A. deltatus*).

Conodonts with coniform elements in the apparatus are not common in the assemblages studied, the most important of them being *Glyptoconus*, probably *G. quadraplicatus* (there is a possibility that "*Oneotodus*" *rotundus* Moskalenko, 1967, is a P element of the same apparatus) (29 specimens in Ang-3; 24 in Ang-2). Hyaline *Drepanodus*-like specimens with the S_0 element distantly resembling *Ulrichodina* may be related to "*Drepanodus*" *concavus* as interpreted by Ji & Barnes (1990).

Of the greatest correlative value are two species of conodonts with incipient denticula-

tion of some elements. The more elaborate of them is *Jumudontus sigmoidalis* (Moskalenko, 1984), different from its cosmopolitan relative *J. gananda* in having a narrow base and sinuous orientation of denticles in P_1 elements (22 specimens in Ang-3; 16 in Ang-2). The Siberian material does not support identification of M elements by Nicoll (1992), who attributed to *Jumudontus* probable specimens of *Protopriodontus*. Instead, associated elements of the Siberian *Jumudontus* have a much less derived appearance (Moskalenko, 1984: pl. 16:18). *Jumudontus gananda* is widespread in the late *Oepikodus evae* Zone of the Arenig. The Siberian species, as suggested by its narrow base, may be transitional between *J. brevis* and *J. gananda* within the same lineage (see Nicoll, 1992), or represents a separate lineage that split out near this point. This interpretation is supported by the co-occurrence of an early member of the *Histiodellella* lineage in Siberia (11 specimens in Ang-3; 9 in Ang-2). *Histiodellella sibirica* (Moskalenko, 1967) (= *Histiodellella angulata* Moskalenko, 1982) may be ancestral to *H. altifrons*, known to occur above the range of *J. gananda* (e.g., Pyle & Barnes, 2003).

Among the numerous relatively shallow-water conodonts reported from the lower Mamyry Formation by Moskalenko (1984), the most distinctive is the pterospathodontid "*Polyplacognathus*" *angarensis* Moskalenko, 1984, of limited vertical distribution, but unknown outside Siberia. Higher up in the section it co-occurs with *Phragmodus flexuosus* Moskalenko, 1973, which indicates the *Pygodus serra* Zone of the Llanvirn.

Angarella is thus known to occur from the Mid Arenig to Late Llanvirn in terms of the British subdivision of the Ordovician.

Phosphatized ellesmeroceratid nautiloids were extracted from a detrital limestone intercalation in the stromatolitic Ust-Kut Formation at Pashino, stratigraphically much below the Badaranovo Formation. Associated specimens of *Cordylodus rotundatus* indicate its own Zone, that is early Tremadoc.

SHELL MORPHOLOGY AND STRUCTURE OF ANGARELLA

The shell of *Angarella* was bivalved, the upper (dorsal) one being of conical appearance and the lower (ventral) almost flat. Dorsal valves are very variable in outline and height of the cone (Figs. 2A, F, H, 3A). The sample taken to the laboratory is too small to offer a reasonable biometric evaluation of variability,

but field observations suggest that there is a complete gradation in the shell geometry. The most common shell outline is oval, somewhat elongate, and with the greatest width at the level of the apex (Fig. 1A). Specimens circular in outline or slightly wider than long also occur. The apex is located in the posterior third of the dorsal valve in most specimens, but it may overhang the margin in the tallest ones (I apply here descriptives as for brachiopod shells, not molluscan conchs). Usually the length of the valve is about 3.5 times its height, but in the tallest specimens it is about 2.5, whereas in the flattest it may reach 4.0.

The apex of the dorsal valve, smooth and hemispherical in shape, is about 1 mm in diameter. Its surface is too crudely preserved, with imprints of sand grains, to allow discrimination of the larval stage.

The ventral valve was cemented to hard objects, as shown by attachment scars replicating the rough substratum surface of undetermined nature. Rarely it is cemented to other *Angarella* shells. Prominent irregular growth increments are discernible on an area of variable extent in the posterior region of the valve. This area is more or less concave, in connection with a slight dorsoventral curvature of the whole valve. Generally, the valve is almost flat and near its posterior margin it attains the greatest thickness. In specimens from marly facies (possibly separate species) this thickness exceeds 1 cm (Fig. 3B).

Shell Structure

The shell thickness is clearly correlated with its mode of growth. Tall-conical specimens are thin-walled (Figs. 2F, G, 3A), whereas low-conical dorsal valves and all ventral valves are thick-walled (Fig. 2H, I).

Internal structures of the *Angarella* shell are well preserved even in strata where aragonitic gastropod conchs are recrystallized into calcitic sparite or dissolved, which proves its originally calcitic composition. There is no evidence of secondary mineralisation or recrystallisation in specimens from Pashino but, as a result of mechanical weathering, the shell is cut by numerous cracks obliterating the original structure. The shell wall structure is laminar and imporous. Because of this structure, the shell matrix of weathered specimens easily splits into fine glossy blades. In the SEM, rhythmic banding is recognizable, with laminae thickness about 1.5 μm (Fig. 3E), with rhythmicity suggestive of daily increments (e.g., Goodwin et al., 2001).

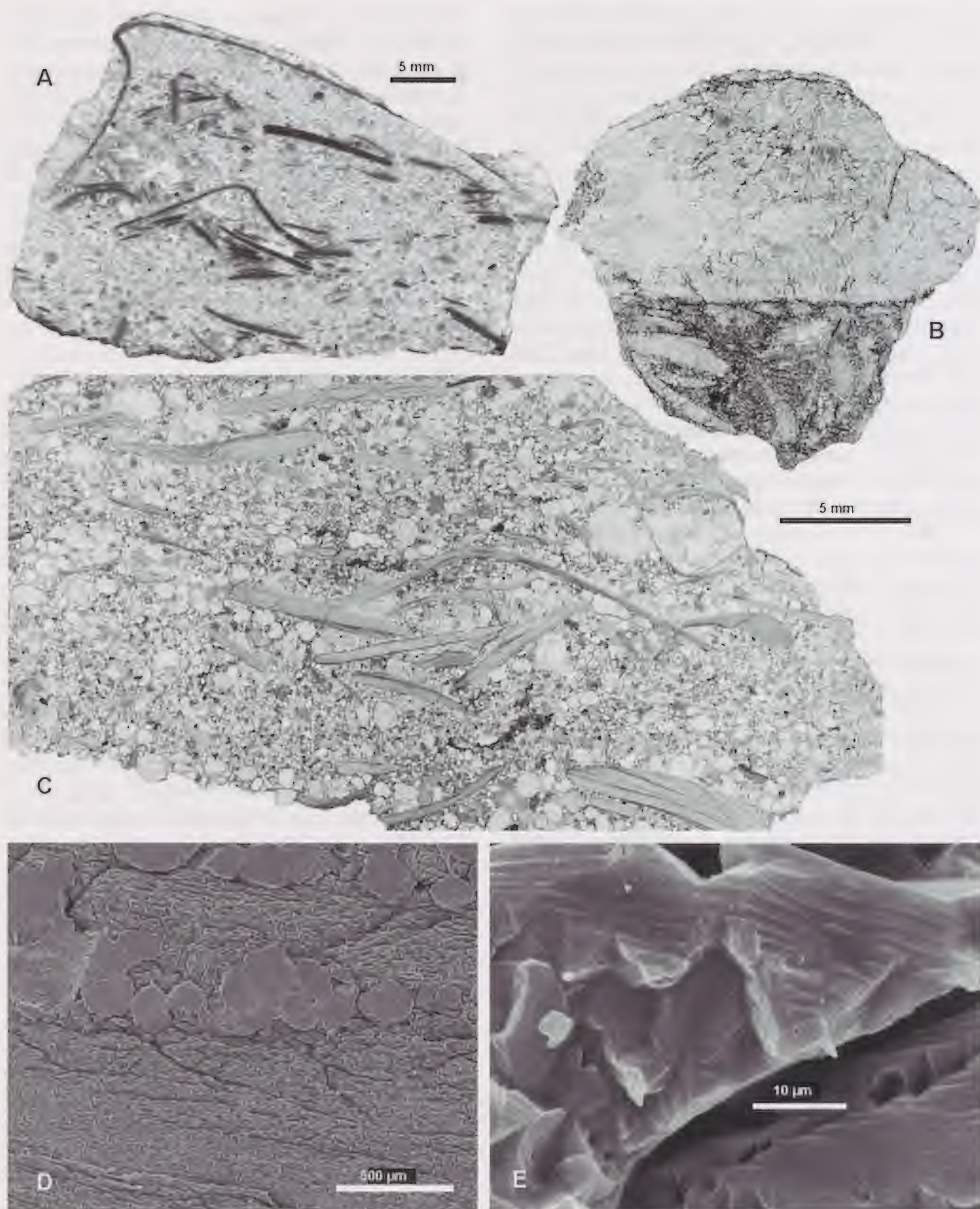


FIG. 3. Wall structure of *Angarella* from the bank of Angara. A, C–E: *Angarella jaworowskii* Asatkin, 1932, high-conical specimen ZPAL Bp 62/24 from the lower Badaranovo Formation at Pashino; polished section (A), thin section showing shell detritus in the sandstone (C), and SEM pictures of shells in transverse section etched with dilute acetic acid (D, E) note polished quartz sand grains in the upper part of the area shown (D) and fine lamination of the shell matrix, possibly daily increments (E); B: Very large and thick *Angarella* sp. ventral valve ZPAL Bp 62/13 from the upper Badaranovo Formation at Rozhkovka; thin section of the anterior margin of diagenetically altered shell; note detritus of thinner parts of shells in the rock matrix below.

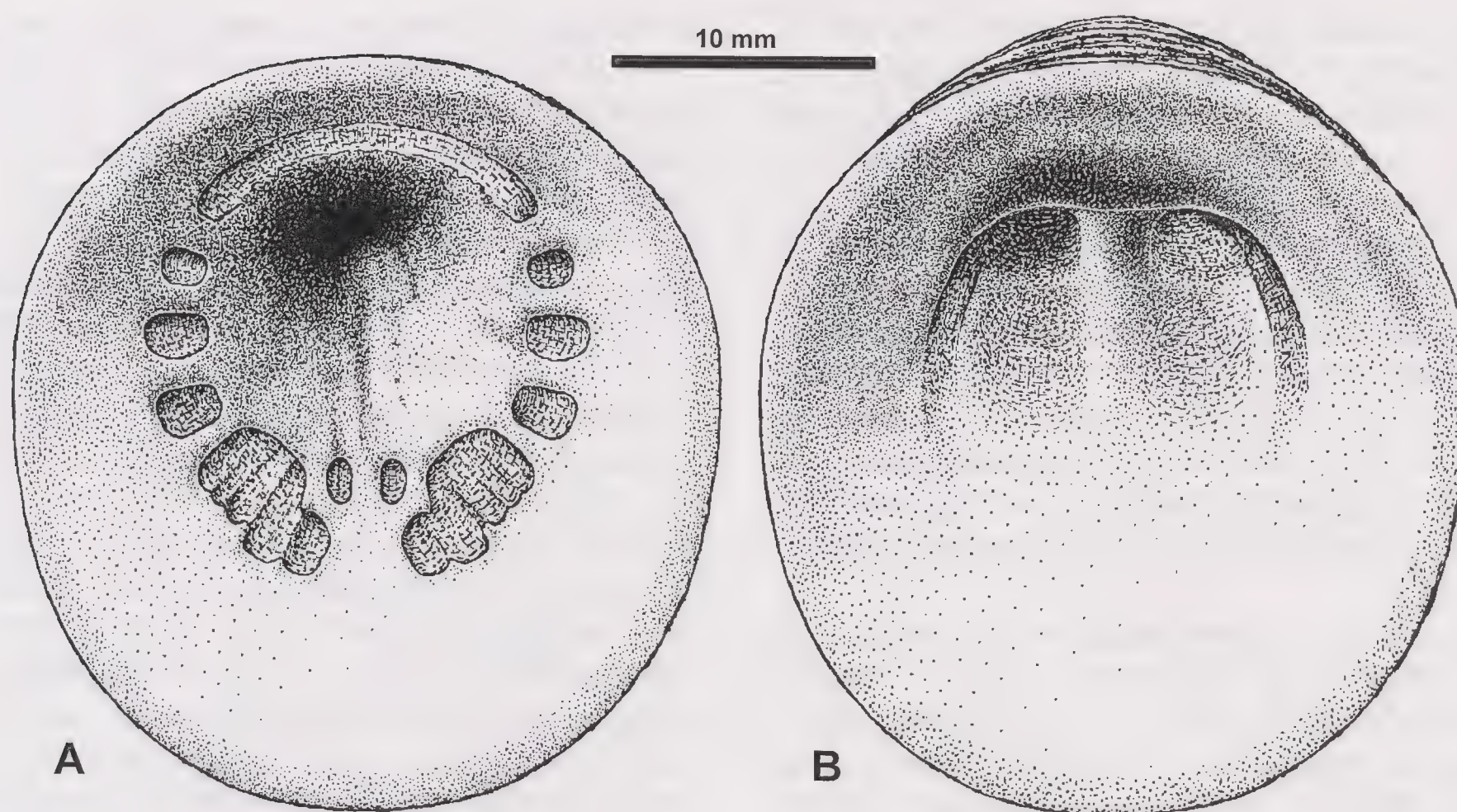


FIG. 4. Restoration of interiors of *Angarella jaworowskii* Asatkin, 1932, from the Badaranovo Formation of the Angara River region, Siberia. A: Interiors of dorsal valves based on ZPAL Bp 62/6; B: Interiors of ventral valves based on ZPAL Bp 62/8.

Muscle Attachments

Muscle attachment scars of *Angarella jaworowskii* were identified and illustrated by Yadrenkina (1984, pl. 8: 1a, b, pl. 9: 3). In her paper, they are shown as large dark-stained fields separated from each other by a narrow strip of lighter matrix. Their exact shape is hard to visualize based on published photographs.

More informative is the part of a mature dorsal valve from the Pashino block split along its internal surface (Fig. 2A–C). The valve represents the flat morphotype that has a relatively thick shell. Consequently, muscle attachment scars are relatively deep for the species. Moreover, roughness of the surface of the muscle attachment area, as compared with the rest of the shell interior, permitted the shell matrix to remain in places on the nucleus, demarcating the limits of muscle attachments. These are symmetrically distributed on both sides of the shell, excluding a possibility of being artifactual.

There are five paired scars and a probably continuous, narrow posterior band. The three lateral scars are of similar size (Fig. 4). A pair of large scars occupies the anteriormost position. These seem to be internally subdivided into smaller fields, perhaps five in each scar. Minute scars are near the midline of the valve at the level of posterior margin of the largest scars.

No ventral valve of comparable quality in representation of muscle attachments is available. The two best preserved specimens with the interior of the valve visible (Fig. 2D, E) show only indistinct areas of muscle attachments. They are clearly delimited by the thickened posterior region of the valve and the low medial ridge. An indistinct, very low transverse elevation may suggest that two pairs of large oval attachments are represented in the posterior part of the ventral valve floor, but their boundaries cannot be traced with confidence. There are two tear-like elongated belts of different coloration along the lateral margins of the valve floor that may also represent muscle attachments. This is definitely not enough to make restoration of ventral attachments reliable, and I hesitate to speculate about the relationship between dorsal and ventral muscle attachments in *Angarella*.

RELATIVES OF *ANGARELLA*

Siberian Species

Conical shells with muscle attachments virtually indistinguishable from those of *Angarella* are known from other rock units of the Early Ordovician and Late Cambrian of Siberia. The stratigraphically and geographically closest is probably *Nyuella bjalyi* Rosov, 1975, col-

lected from sandy limestone near the base of the Ust-Kut Formation of the Kima stage, left bank of the Nyuia River, a tributary of the Lena River. The Ust-Kut Formation underlies the Badaranovo formation in the region, but it is not certain that everywhere they are of the same age. Muscle attachments are preserved as a dark carbonaceous(?) staining (Rosov, 1975) of the same kind as in the *Angarella* specimens of Yadrenkina (1984). There is a possibility that, like the Yadrenkina (1984) material, not all muscle scars are there reproduced with the stain and that these are actually specimens of *Angarella*.

Another form collected from the lower Ust-Kut Formation in the same area is *Lenaella octobinaria* Bjaly, 1973. The type locality is on the Kirenga River, 7 km upstream from Kluchi Village. *Lenaella octobinaria* differs from *Angarella jaworowskii* only in having a taller conical shell with the apex located in its center. It may well be ancestral to the lineage. In fact, Bjaly (1973) reported the species also from the Angara River at Rozhkovo, that is from the same locality from which the material of *Angarella* described here comes. He refers to concentric growth increments on the external surface of the shell, which means that it is preserved in at least some specimens.

The stratigraphically oldest Siberian member of the group and its name-giver is *Kirengella ayaktchica* Rosov, 1968. Its shell form is closely similar to that of *Lenaella*, and the muscle attachments pattern is virtually the same as in *Angarella*. *Kirengella ayaktchica* occurs in sandy limestone of the Khandin Formation on the Kirenga riverbank near the mouth of Ayaktcha stream in the same area of southern Siberia. Based on the co-occurrence of the trilobite *Delgeuloma*, characteristic for the Mansy regional stage, the age of the strata is believed to be Late Cambrian (Rosov, 1968). Specimens frequently preserve the shell, with concentric growth increments visible on the surface and, when the external shell layer is exfoliated, the surface is shiny and smooth (Rosov, 1968: 1429). This description suggests that the shell is of lamellar structure, presumably originally calcitic, as in *Angarella*.

Doguzhaeva (1972) named four species attributed to *Kirengella* and a new genus, *Romaniella*, from the Tremadoc (thus coeval to the southern Siberian Ust-Kut Formation) strata of the southern Urals, on the bank of the Ebit River near the mouth of Kultabasay Creek based on nuclei preserved in sandstone. Muscle scar

attachments there are deep, which indicates reasonable thickness of the shell. Its original mineralogy remains undetermined. Specimens were separated to two genera because on specimens attributed by her to *Kirengella* two additional small anterior (posterior, if the molluscan interpretation is preferred) attachments are discernible. Otherwise the distribution of scars is virtually the same in all specimens. *Kirengella kultavasensis*, based on four specimens, *Romaniella aebitensis*, *R. getlingi* and *R. zverevi* of Doguzhaeva, 1972, are all from the same stratum. By analogy with *Angarella*, with which these Uralian form shares a similar shell appearance, one may suggest that they represent variability in shell form within a single population. Three separate small scars of *Romaniella* appear to correspond to each of the large scars of the anterior pair in *Angarella* and *Kirengella*. The admedial scars are between them, that is, somewhat anteriorward in respect to their position in *Angarella*.

Still within the Siberian Platform but near its northern margin is the type locality of *Moyerokania miagkovae* Rosov, 1970, found on the right bank of the Moyerokan River, a tributary of Moyero, near the mouth of the Superechi Stream. The species is known only from nuclei with muscle attachment scars (Rosov, 1970). They show a characteristic subquadrate outline, with the posterior margin almost straight. *Moyerokania miagkovae* is reported to co-occur with *Angarella*. The main difference between these genera is that in *Moyerokania* admedial scars are located anteriorward of the largest muscle scars.

European Species

Such disposition of muscle attachments characterizes also *Pygmaeoconus porrectus* (Barrande, in Perner, 1903) from the Llanvirn Šárka Formation of Bohemia (Horný, 2006). The shell of *P. porrectus* was thick, highly variable in its geometry and with irregular growth. Interestingly, the shell of this animal was precisely fit to the complex geometry of the substratum. This clearly resulted from its sessile growth mode. The ventral valve was apparently thin or even non-mineralized. A similar fossil, 11 mm long, still attached to the shell of a Mid Ordovician orthoconic nautiloid, was identified as *Archinacella* by Rudolph (1997: 33, fig. 11). The shell aperture in those specimens apparently replicate the substratum morphology, and this may explain unusual geometry of the shell

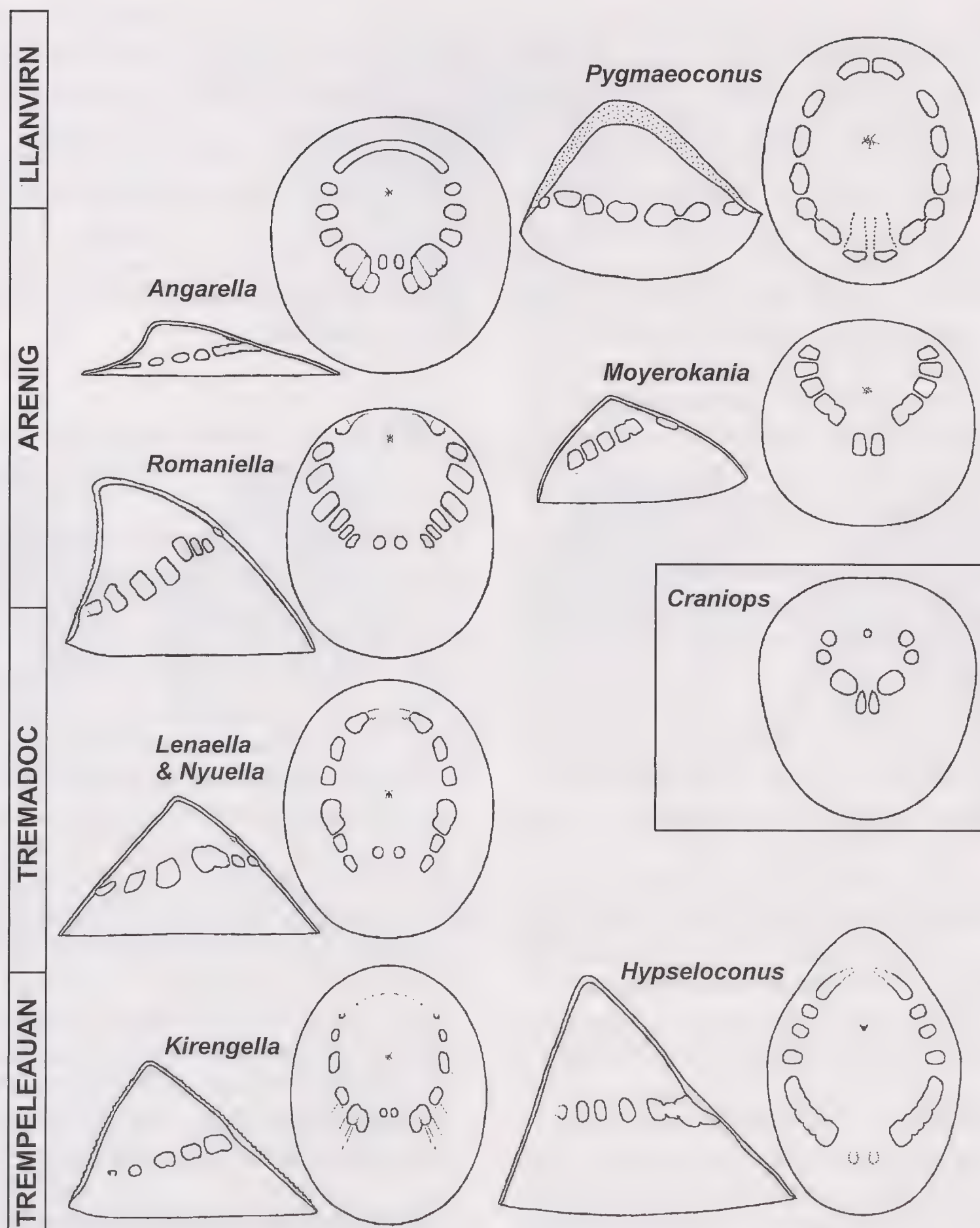


FIG. 5. Stratigraphic distribution of members of the Kirengellidae with known muscle attachments in the dorsal valve; diagrammatic representation of *Craniops* inserted. Restorations of muscle attachments distribution are based on literature sources reviewed in the text.

in the Uralian *Romaniella aebitensis*, to which aspect of morphology Doguzhaeva (1981) paid much attention. She interpreted the presence of a sinus at the adapical shell margin as evidence for a shell curvature opposite to that in *Kirengella*.

North American Midcontinent Species

Pygmaeoconus is geologically younger than *Romaniella* and *Moyerokania*, and the anterior disposition of its admedial attachment scars may be a derived character. If so, the alleged

patellacean gastropod *Floripatella rousseaui* Yochelson, 1988, from the Whiterockian Kanosh Shale of Utah may be even more derived. Numerous muscle attachments form there an almost continuous horseshoe belt (Yochelson, 1988).

Serial muscle scars associated with conical shell shape have also been identified by Stinchcomb (1980) in another North American form, *Hypseloconus* cf. *H. stabilis* Berkey, 1898, from the Late Cambrian Davis Formation of Missouri. Although rather superficially described, the disposition of muscle attachments in this

form seems similar to that in the type species of *Kirengella*, and because of this Webers et al. (1991) and Stinchcomb & Angeli (2002) placed *Hypseloconus stabilis* Berkey, 1898, and other American species earlier classified in this genus in *Kirengella*, namely *H. washingtonensis* Stinchcomb, 1975 (nom. corr. herein; *Hypseloconus* is of masculine gender, not neuter), and *H. simplex* Berkey, 1898. Stinchcomb & Angeli (2002) also added to *Kirengella Hypseloconus compressus* Ulrich & Bridge, 1931, *H. ozarkensis* Ulrich & Bridge, 1931, *Gasconadaeconus expansus* Stinchcomb, 1986, and *Kirengella oregonensis* Stinchcomb & Angeli, 2002. The family Kirengellidae was supplemented with his new genus and species *Irondalia irondalensis*. These all are forms of generalized morphology with unknown musculature, and their congenerity with *Kirengella* does not seem well substantiated.

If these nomenclatorial transfers were accepted, the muscle scars of true *Hypseloconus* (its type species is *H. recurvus* Berkey, 1898), as well as the original shell mineralogy, would remain unknown. However, shells of all the American species differ from the Siberian type species of *Kirengella* in being much taller, having an ovate cross-section and an anteriorly displaced apex. In stratigraphically higher Emence and Gasconade Formations of Trempealeauan and earliest Ordovician age in Missouri more elongate and septate *Shelbyoceras* occurs. Muscle scars are unknown in it, but general shell form makes the ancestor-descendant relationship between *Hypseloconus* and *Shelbyoceras* likely. The North American lineage is likely to be separate of the Siberian one. A wide range of hypseloconid shell morphologies is known in the North American Midcontinent province (Greenland) as early as in the late Mid Cambrian (Peel, 1988).

The only other Cambrian fossil shell with preserved serial muscle attachments is that identified as *Scenella* sp. undet. by Rasetti (1954; Peel, 1991: 56). The almost centrally located shell apex and the arrangement of muscles make it more similar to the kirengellids than to the tergomyan monoplacophorans. In the latter, the “muscle scars form a ring located posterior to the shell apex, such that the apex lies outside of the muscle field” (Peel, 1991: 14).

The unavoidable consequence of the above review is that the family-rank taxa Hypseloconidae Knight, 1956, Kirengellidae Starobogatov, 1970, Romaniellidae Rosov, 1975, Hypseloconellacea (*recte* Hypseloconacea) Stinchcomb, 1986, and Pygmaeoconinae Horný, 2006, are

subjective synonyms. The same refers to the orders Kirengellida Rosov, 1975, Romaniellida Doguzhaeva, 1981, and Hypseloconida Peel, 1991. Ironically, the arrangement of muscle attachments in the Kirengellida is rather different from that in unquestionable Monoplacophora, which appear to be unknown before the Late Ordovician. Instead, there are some Cambrian fossils exhibiting much similarity to the kirengellids in this respect.

CAMBRIAN PROBLEMATICA POSSIBLY RELATED TO ANGARELLA

In the Early Cambrian several species of phosphatic shells with muscle attachment scars of disposition similar to that in *Angarella* occur (Fig. 6). They are referred to as mobergellans (e.g., Conway Morris & Chapman, 1997; Skovsted, 2003) with the family name Mobergellidae Missarzhevsky, 1976, available. Although originally described as brachiopods, they are known exclusively from their “dorsal” valves that make such affinity difficult to support. Their brachiopod affinities are generally also considered unlikely because in some species shells are concave, which makes them similar rather to opercula of tubular skeletons (Bengtson, 1968). No such tubes fitting mobergellid and co-occurring with them have been identified yet.

However, some mobergellans have high vaulted shells (e.g., *Aktugaia* and *Thorslundella*) and with irregular outline and growth bands distribution making them similar to the kirengellids such as *Pygmaeoconus*. The lack of ventral valves in fossil assemblages could have resulted from their being unmineralized or cemented to hard bottom environments not represented in the fossil record. A taphonomic analogue may be offered by the Ordovician acrotretid *Eoconulus*, which cemented to the substratum by its ventral valve. Although its phosphatic dorsal valves are common fossils, known after incomparably more numerous specimens than mobergellas, it took some time until the rare ventral valve was identified (Holmer, 1989: 147). One may speculate that the ventral cementing valve of mobergellans was flat or reduced in a manner suggested here for the kirengellid *Pygmaeoconus*.

Despite the similarity in overall form, the phosphatic composition of the mobergellans makes them basically different from the kirengellids. The difference is original (Nyers, 1987; Skovsted, 2003), because at least in *Aktugaia triangula* Missarzhevsky, 1976, from

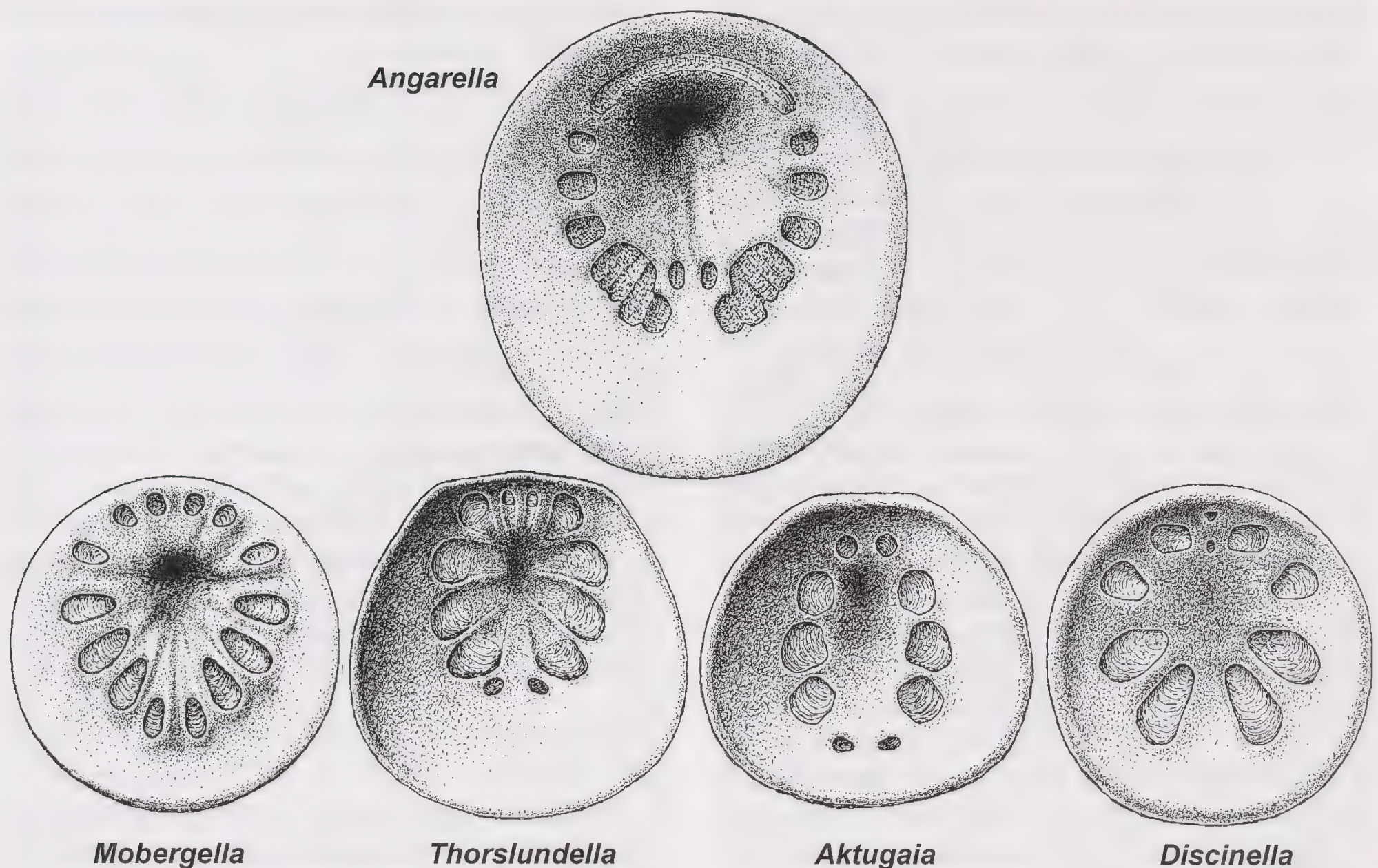


FIG. 6. Comparison of muscle attachments in the dorsal valve of *Angarella* with those of various members of the Mobergellidae. Restorations are based on literature sources reviewed in the text.

the Geres Member of the Shabakhty Formation in Malyi Karatau Range, Kazakstan, the shell differs from secondarily phosphatized co-occurring mollusk shells in its shiny appearance (Skovsted, 2003).

Genera of the mobergellans differ from each other in number of muscle attachments (Skovsted, 2003). The pattern of attachments, with a circle of oval attachments surrounding apex, makes them remotely similar to the “cyclomyan” bellerophontids, and such affinity has been proposed for them by Nyers (1987). However, in their roughly similar size decreasing posteriorly (brachiopod orientation applied), and the presence of a pair of distinctly smaller scars at the anterior end, they more closely resemble the pattern represented in the kirengellids. The small anterior attachments pair are in the ring, thus in position like *Hypseloconus* rather than *Kirengella*. There is a long time span separating the oldest kirengellids from the mobergellans, which makes a relationship between them only a highly hypothetical possibility. However, the mobergellans remain the only fossil organisms preceding the kirengellids with a similar body plan.

BRACHIOPOD AFFINITIES OF *ANGARELLA*

Originally *Angarella* was attributed to the Craniidae. This affinity was questioned by Yadrenkina (1984), because, unlike recent craniids, the four pairs of large muscle attachment scars she identified inside the dorsal valve of *Angarella* leave only one third of the internal shell volume for the mantle cavity. She noticed that there was virtually no space for the lophophore and that the virtually flat ventral valve did not protect the animal against ingestion of the mud from the sea bottom. Therefore, she proposed that *Angarella* represents a new unknown group of animals with bivalve shells of the brachiopod ground plan.

Lophophore of *Heliomedusa*

The problem of the space for the lophophore in the shell of *Angarella*, raised by Yadrenkina (1984), has been indirectly solved by *Heliomedusa*, an Early Cambrian mickwitziid (Holmer & Popov, 2007) with a thin organic or organophosphatic shell. This brachiopod had a surprisingly simple lophophore, with a row of

radially oriented tentacles forming a relatively narrow belt along the anterior part of the shell. Its extent was virtually the same as, or at least closely similar to, the area outside the muscle scar belt in *Angarella* (Chen et al., 2007: fig. 3: 4). A large visceral mass may be plesiomorphic for brachiopods, as suggested by its entering the base of the pedicle in some Early Cambrian lingulids (Zhang et al., 2005, 2007; Holmer & Caron, 2006). *Heliomedusa*, as restored by Chen et al. (2007), had a simple organization of adductors, with a pair of large anterior and another pair of small posterior muscles surrounding the large visceral mass with pedicle in the center. Although *Heliomedusa* is not a craniopsid, its ancestral position with respect to craniopsids and perhaps also kirengellids seems likely (at least it is a more parsimonious solution than assuming completely independent origin of calcareous and organophosphatic skeletons). Transition from a shortened pedicle to shell cementation may have occurred in a way analogous to the shift from a massive shortened byssus to cementation in the anomiid bivalves (Fürsich & Palmer, 1982).

Kirengellid and Craniopsid Shells

Apart from the disposition of the dorsal valve muscle attachments, the *Angarella* shell is similar to that of the craniopsid inarticulate brachiopods. In particular, the general appearance of shells of the Devonian *Lingulapholis*, free lying on the sediment surface in its postlarval stage, is like that of *Angarella*. The Mid to Late Ordovician (Caradoc-Ashgill) *Pseudopholidops* differs from *Lingulapholis* only in the distribution of muscles, whereas *Craniops* (Caradoc-Tournaisian) was attached apically by cementation (Popov & Holmer, 2000).

The calcitic secondary shell of *Craniops* has a laminar structure (Williams, 1997: fig. 249.1), thus similar to that of *Angarella*. The *Angarella* shell matrix shows increments similar to those in the Ordovician *Petrocrania* (Cusack & Williams, 2007: fig. 1648a) or Recent *Novocrania* (Cusack & Williams, 2007: fig. 1644). It is possible that the shell of *Angarella* underwent some diagenetic changes of a similar kind as those in fossil craniids, but its originally calcitic and laminar structure seems to be not in doubt, being visible in thin sections, on etched surfaces and in the pattern of exfoliation. Under SEM, the shell matrix of *Angarella* (Fig. 3E) shows growth banding resembling that in the primary calcitic shell layer of brachiopods, for instance

in the advanced Recent *Notosaria* (Williams et al., 1997: fig. 11.1).

The main and possibly fundamental difference between the Craniopsida Gorjansky & Popov, 1985, and the Kirengellida is in the distribution of shell muscles. In *Angarella*, instead of three pairs of lateral muscle scars recognized in *Craniops* (Popov & Holmer, 2000), there are four. Instead of the single posterior attachment there is a posterior belt. Presence of paired posterior and anterior adductors is considered plesiomorphic to all brachiopods by Holmer et al. (1995) and rather conservative in their evolution. If the kirengellids are truly brachiopods, a secondary complication of their musculature took place in their early evolution, perhaps in connection with cementation to the substratum and under selection pressure, of a kind similar to that acting on limpet-like molluscs.

Ancestry of Kirengellids

To resolve the question of the origin of the discrepancy in musculature, the evolution of the kirengellids and craniopsids has to be traced backward up to the identification of their putative common ancestor. This does not seem possible at the moment.

Probably the geologically oldest craniopsid with well-known musculature is *Pseudopholidops stolleyana* (Huene, 1900) from the Caradoc (Baltic Nabala-Vormsi stages) of Belorussia (Popov & Pushkin, 1986). It is still much younger geologically than the last kirengellids. Juvenile shells with a shape similar to those of *Angarella* from the latest Early Ordovician (Kunda-Aseri boundary) were tentatively attributed to the craniids (Madison, 2007). The craniids, which are more derived than craniopsids, are known already from the Tremadoc (Mergl, 2002; Sdzuy et al., 2001), which implies a “ghost” lineage of the craniopsids exists before this date. Only putative craniopsid relatives, with strongly convex larval shell, are known from the Early Cambrian Upper Bastion Formation of Greenland (Skovsted & Holmer, 2005). Other Cambrian brachiopods with calcareous shells (Balthasar, 2008) are rather unlikely to be related to the craniopsids or kirengellids.

A possibility remains that the mobergellans are near the ancestry of both the craniopsids and kirengellids. The Mid Cambrian *Scenella* of Rasetti (1954) may represent the connecting link, although it is too incompletely known for this purpose. The mobergellan and kirengellid

anterior admedial pair of small muscles would represent the brachial protractor (Popov & Holmer, 2000), homology of other muscles remaining obscure (Fig. 6).

The difference in shell composition may not be of great importance, as in the early brachiopods organic, phosphatic, aragonitic and calcitic shells are known, and the gap between lineages characterized by different skeletal mineralogy does not need to be wide (Balthasar, 2008). This is suggested also by the apparent craniopsid affinities of the trimerellid brachiopods with presumably originally aragonitic shell (Gorjansky & Popov, 1985, 1986). Probably also shells of some of the kirengellids were aragonitic. This could have been the case with unnamed forms I collected from the upper part of Ust-Kut Formation at Angara near Kudinsk and the Krivaya Luka Formation at the Lena River. In shell shape they are similar to *Kirengella* or even taller, resembling the North American *Hypseloconus*. They frequently show their shell matrix recrystallised into calcitic sparite, as if originally aragonitic. Obviously, a possibility remains that the aragonitic *Kirengella*-like Ordovician fossils are truly monoplacophorans. Nevertheless, additional evidence for this has to be provided, as the serial distribution of muscle attachment is misleading.

Whether the bivalved kirengellids are brachiopods or not, they have to be removed from considerations on the early evolution of mollusks, in which these fossils were assumed to play the main role. It appears that the pre-Late Ordovician history of the tergomyan Monoplacophora has to be rewritten. More specifically, the brachiopod affinity of the celebrated high-conical *Hypseloconus* calls for reconsideration of the theory about the ancestry of Cephalopoda.

ORIGINS OF THE CEPHALOPODS

It is generally accepted that the body plans of cephalopods, monoplacophorans, and basal gastropods are closely similar. There is a significant progress in understanding the origin and early evolution of the nominal cephalopod organs: head and arms. Embryological evidence is now available that the unique digital tentacles of *Nautilus* or arms of other cephalopods developed from the foot of an ancestral mollusk (Shigeno et al., 2008). Comparative anatomical data suggest that the adhesive function of carbohydrates and proteins secreted on tentacles of *Nautilus* was probably gradually taken over

by muscular suckers in more advanced forms (von Byern & Klepal, 2006). Such interpretations of the evolution of soft parts are difficult to test with the paleontological evidence, but the modifications of shell in the evolution of cephalopods have a rather good fossil record. An exception is the origin of the phragmocone, which probably took place not later than in the early Late Cambrian. In this respect we have to rely only on speculations.

Peel (1991) reaffirmed Yochelson et al.'s (1973) hypothesis that cephalopods originated from a benthic monoplacophoran similar to *Hypseloconus*. Based on endogastric curvature, he proposed aenigmatic helcionellid molluscs as possible ancestors to the cephalopods, the idea supported by molecular phylogenetic proximity of scaphopods (probable distant successors of the helcionellids) to cephalopods (Steiner & Dreyer, 2003). The main argument used by Yochelson et al. (1973) and Webers & Yochelson (1989) was the presence of diaphragms (septa) in the apex. Dzik (1981), Chen & Teichert (1983), and Teichert (1988) pointed out that it is the siphuncle, not septa, that makes a cephalopod and that septa occur widely in high-conical shells of unrelated invertebrates. Cephalopods from the beginning of their palaeontologically documented history differ from the monoplacophorans in the shape of their larval shells. In their subspherical apex and cylindrical appearance, they resemble rather larval shells of gastropods. A flat discoidal larval shell is known to occur in the tryblidiid monoplacophorans at least since the Silurian (Dzik, 1994: 294, fig. 30A). Possibly they had such shells already in the Early Cambrian, although mollusks of that age with low cap-like larval shells have not been shown to have serial pedal musculature (Dzik, 1994: 265, fig. 12A). Such shell morphology of the Cambrian limpet-like mollusks means that the early development within the egg capsule without free-living larva characterized tryblidiid monoplacophorans for all their evolution. Thus, according to the Yochelson et al. (1973) theory, the pelagic mode of life was a complete novelty in the lineage of benthic monoplacophorans adapted to life among stromatolites. Such was the ecology of *Hypseloconus* and related forms (Stinchcomb, 1975) interpreted as molluscs.

On the contrary, I proposed (Dzik, 1981) that the origin of the phragmocone in the early evolution of cephalopods was a result of extension of the pelagic mode of larval life of their ancestors to mature stages, in a way similar to pteropods. I suggested that the

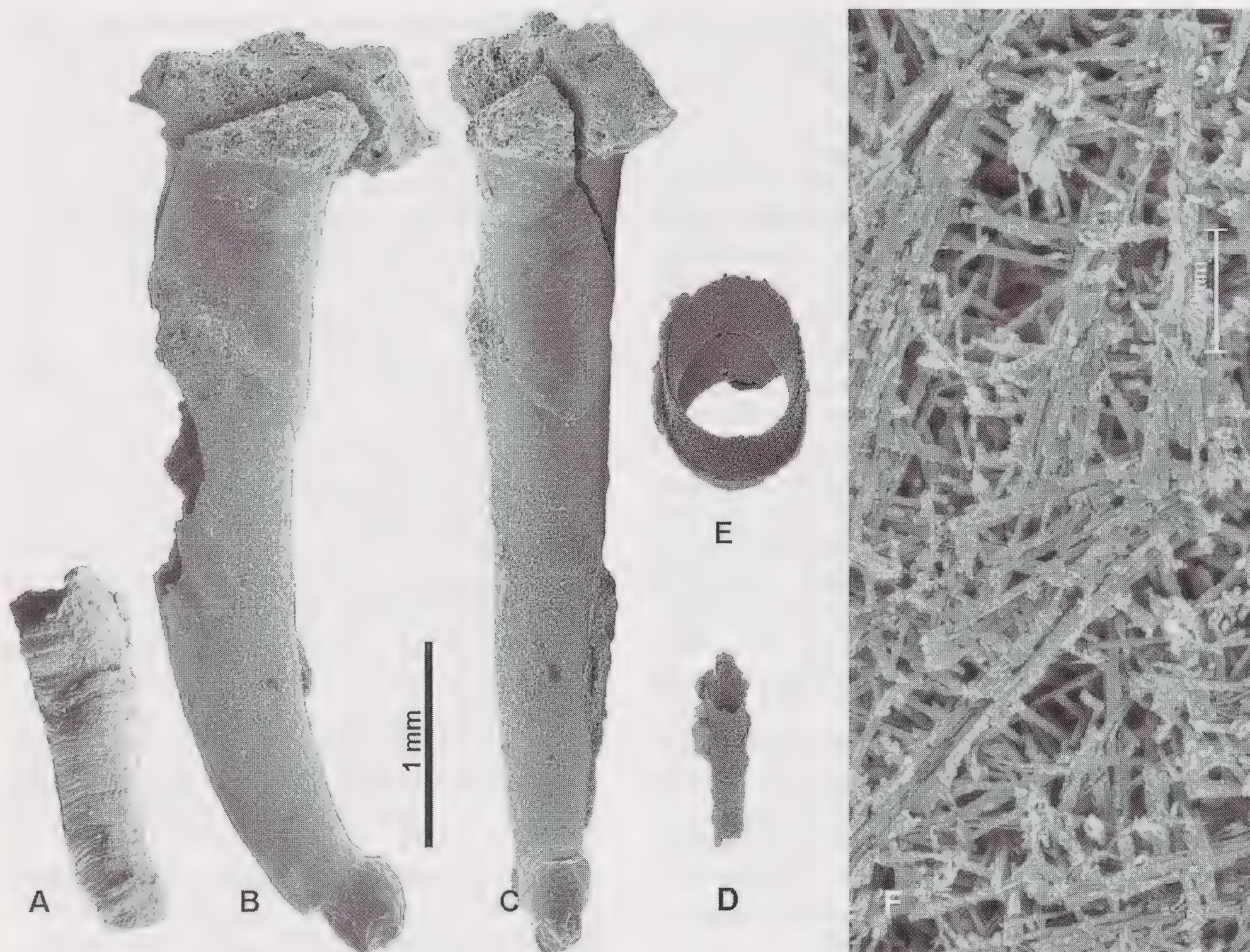


FIG. 7A–C. Possible relative of earliest cephalopods, *Turcutheca crassaecochlia* Syssoiev, 1962, from the Tommotian (*Dokidocyathus lenaicus* Zone) at Bydyangaia on the Lena River, central Yakutia; phosphatized specimens photographed under SEM. A: Specimen with well preserved surface of embryonic part (destroyed while removed from the stub); B, C: Probably mature specimen (largest known) with partially phosphatized shell wall and displaced embryonic part preserved as glauconitic internal mold, lateral and posterior ('ventral') views; D–F: Pieces of phosphatized siphuncles (mineralized fibres of the connecting ring enlarged in F) of ellesmeroceratid nautiloids from the earliest Ordovician (early Tremadoc) Ust-Kut Formation at Pashino, Angara River, southern Yakutia; note that inferred larval conch size was similar to that of *Turcutheca* but mature specimens were many times larger.

positive buoyancy by replacing liquid with gas in the phragmocone chambers (Greenwald et al., 1982, 1984; Greenwald & Ward, 1987) was preceded by a plain removal of sodium ions from the liquid inside the conch tip as a result of the siphonal epithelium sodium pump action, in a way analogous to that of the Recent cranchiid squids. This requires that the cephalopod ancestor already had a pelagic veliger-like larva with subspherical embryonic and cylindrical larval conchs. Such conchs characterized the orthoceratid and presumably also ellesmeroceratid cephalopods (Dzik, 1981); note that the smallest piece of the oldest known Late Cambrian cephalopod *Plectronoceras* was less than 1 mm in diameter (Webers

& Yochelson, 1989: fig. 3), which suggests the presence of a minute pelagic larva. From the earliest Ordovician Ust-Kut Formation at Pashino fragmentary phosphatized conchs of ellesmeroceratid nautiloids were recovered with siphuncle diameter 160 μm ; the conch apex diameter was thus less than 0.8 mm. The size of the embryonic conch was not much larger than in other early mollusks. Larvae with elongate cylindrical conchs were also typical for the Cambrian bellerophonitids, gastropods, and hyoliths (Dzik, 1994).

Possible ancestors of the lineage leading to the cephalopods are known from the Early Cambrian. *Turcutheca* is an Early Cambrian mollusk with the general conch form closely

resembling that of the earliest ellesmeroceratid cephalopods: endogastrically curved and laterally compressed, with relatively large subspherical embryonic part (Fig. 7). As usual for any high-conical shells, diaphragms may occur in the apex of *Turcutheca* or related forms, but no sign of anything similar to a siphuncle is known. Despite its unusual conch form *Turcutheca* seems related to hyoliths (they have a depressed and straight or exogastric conch). Perhaps it had a morphologically simple calcified operculum, like its relative *Ladatheca* (Dzik, 1994: 268). If it is truly related to cephalopods, not only did the siphuncle have to develop in the course of evolution to the Late Cambrian cephalopods but also the size of the conch, both mature and embryonic, had to increase. Together with reduction of the foot, the operculum was probably transformed into the lower jaw (Dzik, 1981; the idea presented also without attribution to its source in Seilacher, 1993).

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ANATOMY OF THE TIPHOBIINI FROM LAKE TANGANYIKA (CERITHIOIDEA, PALUDOMIDAE)

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ABSTRACT

The anatomy of five poorly known endemic species of paludomids – *Bathanalia straeleni*, *Chytra kirkii*, *Limnotrochus thomsoni*, *Mysorelloides multisulcata*, *Paramelania iridescens* – from Lake Tanganyika is described. This assemblage, currently united in the Tiphobiini, is loosely characterized by a more or less trochiform shell shape and a mostly oviparous life mode. However, only scant information on the anatomy is available in the literature. Despite significant conchological variability, anatomical investigations reveal overriding similarity in features of the alimentary system (radula, midgut), kidney, and reproductive anatomy. *Bathanalia* and *Mysorelloides* are found to share features of the ovipositor, esophagus and spermatophore bursa; *Chytra* and *Limnotrochus* share features of the salivary glands and spermatophore bursa. *Paramelania* remains a clear outlier in shell morphology, but shares several likely plesiomorphic features of the operculum, midgut and nervous system with *Tiphobia*. Unlike other morphologically distinct clades of Lake Tanganyika paludomids, no unique anatomical character was found that unambiguously unites the Tiphobiini.

Key words: freshwater, morphology, shell, alimentary system, reno-pericardial system, nervous system, reproductive system.

INTRODUCTION

The spectacular endemic species assemblage of phenotypically diverse paludomid gastropods in Lake Tanganyika comprises approximately 70 species (Michel, 2004). As discussed elsewhere (Glaubrecht, 1996, 1999, 2008; Strong & Glaubrecht, 2002), the divergent conchological features of Lake Tanganyika gastropods, combined with inadequate knowledge of their internal anatomy, have left their mark in a chaotic and confusing classification. What little anatomy was known was too unremarkable to reveal their true affinities and was easily misconstrued.

The first series of anatomical papers was published around the turn of the century (Moore, 1898, 1899a, b, 1903; Digby, 1902), and remained all that was known of these forms for roughly 50 years until the Belgian hydrobiological mission to the lake in 1946–1947. This period of renewed interest resulted in the publication by Leloup (1953) that documented the operculum and radula of numerous lake gastropods, many for the first time, and sev-

eral anatomical studies (Mandahl-Barth, 1954; Bouillon, 1955). This was followed again by a long hiatus until the modern age of investigation, which has yielded a series of anatomical and molecular studies (West & Michel, 2000; Michel, 2004; Wilson et al., 2004; Strong & Glaubrecht, 2002, 2003, 2007, 2008; Glaubrecht & Strong, 2004, 2007).

Despite this long history of inquiry, many of these endemic gastropods remain poorly known, some more than others, including a loose-knit group of oviparous and ovoviparous species with more or less trochiform shells currently classified with *Tiphobia horei* Smith, 1880, in the Tiphobiini Bourguignat, 1886 (Bouchet & Rocroi, 2005): *Bathanalia straeleni* Leloup, 1953; *Chytra kirkii* (Smith, 1880); *Limnotrochus thomsoni* Smith, 1880; *Mysorelloides multisulcata* (Bourguignat, 1888); and *Paramelania iridescens* (Moore, 1898). With the exception of *Tiphobia horei*, which was recently redescribed (Strong & Glaubrecht, 2007), virtually nothing is known about these species. Available anatomical descriptions of *Chytra kirkii*, *Limnotrochus*

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thomsoni, and *Paramelania iridescens* were published over a century ago and are woefully incomplete (Digby, 1902; Moore, 1898, 1899b, 1903). Only scant information on the radula and operculum are known for *Bathanalia straeleni* and *Mysorelloides multisulcata* (Leloup, 1953). While the congener *Bathanalia howesi* Moore, 1898, has been included in molecular analyses (West & Michel, 2000; Michel, 2004), *B. straeleni* has not, and no sequences are available for *Mysorelloides*, rendering any anatomical information all the more critical for understanding its affinities.

Although not always reflected in their classification, suggested affinities of tiphobiines have been rooted in their conchological attributes. *Limnotrochus* and *Chytra* possess shells that closely approximate a typical trochoid construction (Smith, 1881; Ancey, 1882; Yonge, 1938). *Bathanalia* and *Mysorelloides*, while not as solid and lacking the nodulose ornament, possess similarly umbilicate shells. The ovoviviparous *T. horei* possesses a shell that is umbilicate in juveniles, with a prominent keel similar to *Limnotrochus*, *Chytra* and *Bathanalia*, and produces spines along the keel like *Bathanalia howesi*. *Paramelania*, with its rather high, conical spire, thickened holostomous aperture, rounded whorl profile, and lacking an umbilicus, is the least well accommodated among this assemblage.

Consequently, *Chytra* and *Limnotrochus* have been cited as closely related, *Bathanalia* with *Tiphobia*, and *Paramelania* acknowledged to resemble *Lavigeria*, but classified in an isolated position based on shell, operculum and radula characters (i.e., “*Limnotrochus* group”, “*Tiphobia* group”, and “*Paramelania* group”, respectively; Pilsbry & Bequaert, 1927). Thiele’s (1929–1935) classification marked a significant departure from previous views, uniting the tiphobiine taxa with *Bridouxia*, *Reymondia*, *Spekia*, *Stanleya*, *Stormsia* and *Tanganyicia* in a Tribe Paramelaniini, but he failed to recognize nomenclatural priority of the family-group name Tiphobiidae Bourguignat, 1886, for this assemblage. Recently, Bandel (1998) proposed a classification that reinstated the isolated positions of *Paramelania* and *Tiphobia* in separate subfamilies citing features of the shell, operculum, radula and reproductive modes (oviparous vs. ovoviviparous) and tentatively suggested that *Bathanalia*, *Chytra*, *Limnotrochus* and *Mysorelloides* may be united, but that current knowledge did not allow assigning them to one of the recognized subfamilies. In contrast, Glaubrecht (2008) largely followed Thiele’s

concept of Paramelaniini, united by the presence of a concentric operculum with a spiral nucleus, but subgroups within this assemblage were distinguished by radular morphologies and similar radulae were assumed to have arisen in parallel in other subfamilies.

Molecular analyses have generally supported tiphobiine taxa as closely related, although taxon sampling of different studies has not been comparable, and no molecular sequences are available for *Mysorelloides*. In an analysis of partial mitochondrial COI sequences, West & Michel (2000) found support for a clade with available tiphobiine taxa – *Bathanalia*, *Chytra*, *Limnotrochus*, *Paramelania*, *Tiphobia* – but which also included *Anceya* and sometimes *Lavigeria*. However, anatomical studies (Strong & Glaubrecht, 2007, 2008) demonstrate the distinctiveness of the latter two and that their affinities likely lie elsewhere. In an analysis of partial mitochondrial 16S and COI sequences with a larger subset of lake taxa, Wilson et al. (2004) recovered a clade uniting *Limnotrochus*, *Paramelania* and *Tiphobia*, but *Bathanalia*, *Chytra* and *Mysorelloides* were not sequenced. Michel’s (2004) results, based again on partial COI sequences, supported a monophyletic Tiphobiini (excluding *Mysorelloides*). This molecular evidence, in the context of available morphological data including that presented herein, formed the basis for the classification in Bouchet & Rocroi, which acknowledged that the Tiphobiini may be paraphyletic (Strong, pers. comm. in Bouchet & Rocroi, 2005: 275). The goal of this contribution is to explore this anatomical data and to assess the relationships suggested by molecular data in an anatomical context.

MATERIAL AND METHODS

Anatomical Descriptions

The scarcity of well-preserved alcohol material in museum collections has been an impediment to anatomical investigations of Lake Tanganyika gastropods. For some species, alcohol preserved material is rare (*Bathanalia straeleni*, *Mysorelloides multisulcata*, *Chytra kirkii*), for others the alcohol material is of poor quality, typically reflecting the fact that specimens were placed in preservative without cracking the shell. For small species, specimens placed whole into alcohol are often salvageable as the volume of tissue is small. But for large species, if the shell is not broken they can be too poorly

preserved for even basic anatomical observations. In the present investigation, only a single female of *B. straeleni* (IRSNB), two females of *M. multisulcata* (IRSNB), and a single male and female of *C. kirkii* (IRSNB, USNM) were available for study from museum collections. Study of *Limnotrochus* and *Paramelania* was based on recent collections by Klaus Bandel (Hamburg) and MG in 1995, Anthony Wilson (Zurich) in 1999 and 2000, and by Heinz H. Büscher (Basel) in 2003, but only one of these specimens was cracked prior to fixation; two females and one male were examined for *Limnotrochus thomsoni* and for *Paramelania iridescens* four specimens were dissected, but only one had an adequately preserved midgut and only two had adequately preserved gonoducts to allow accurate descriptions. Specimens were examined using Leica MZ 9.5 or MZ 12.5 binocular microscopes with *camera lucida*; visualization of structural details was enhanced with aqueous toluidine blue.

Formula for radular tooth descriptions is as follows: (1) rachidian: number of denticles on left side/median cusp/number of denticles on right side, (2) lateral teeth: inner denticles/pronounced cusp/outer denticles, (3) marginal teeth: number of denticles on inner marginal tooth/number of denticles on outer marginal tooth.

Midgut investigations were completed by making an incision around the exposed periphery of the midgut chamber along the right, anterior and posterior margins and deflecting the roof to the left.

Museum Codes

AMS	Australian Museum, Sydney, Australia
CM	Carnegie Museum, Pittsburg, Pennsylvania, U.S.A.
BMNH	The Natural History Museum, London, U.K.
DBL	Danish Bilharziasis Laboratory, Charlottenlund, Denmark
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MRAC	Musée Royal de l'Afrique Central, Tervuren, Belgium
NHMB	Naturhistorisches Museum, Basel, Switzerland
ZMB	Museum für Naturkunde, Leibniz Institute for Research in Evolution and Biodiversity, Berlin (formerly Zoologisches Museum Berlin), Germany

RESULTS

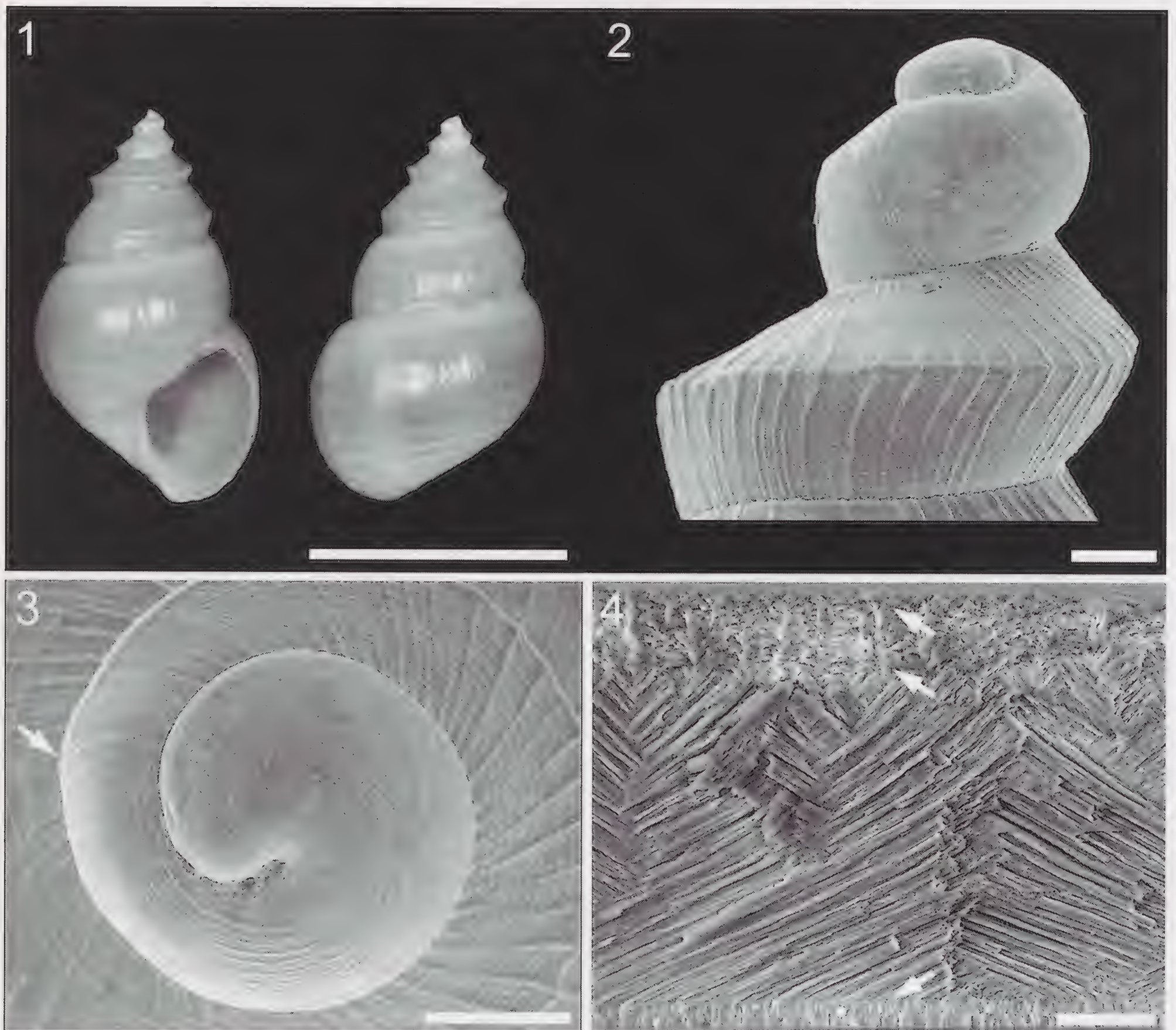
Bathanalia straeleni Leloup, 1953

Material Examined: Democratic Republic of Congo: off Cape Bwana n'Denge, 1,000 m offshore along the coast, trawling starting 3 mi [4.83 km] NW of Lugumba until in front of Lukuga River, 20–80 m (IRSNB no. 50) (1 “paratype” dissected = syntype, as no (holo) type was designated by Leloup, 1953); Katibili Bay, 500 m from the river, 65–70 m (IRSNB no. 133) (58 spms); Bracone Bay, Kavala Island, 12 m (IRSNB no. 138) (16 spms). Tanzania: Utinta Bay, 45–65 m (IRSNB no. 127) (1 spm); bay to the south of the Malagarasi River (IRSNB no. 143) (2 spms).

Shell: Adult shell comprising up to seven whorls (Fig. 1). Apical cap of embryonic shell with irregularly, finely textured surface, rapidly giving way to numerous fine spiral threads (Figs. 2, 3). Gradual transition to teleoconch marked by development of regular, thick axial threads, peripheral keel at shoulder and basal spiral cord sometimes visible just above suture. Early teleoconch whorls angular. Axial elements forming nodes at intersection with keel. Basal cord joined on later teleoconch whorls by variable number of smoothly undulating spiral cords on lower half of whorl. Keel and nodular ornament gradually diminishing, producing flatly rounded later teleoconch whorls with fine, sigmoidal growth lines and basal spiral cords. Aperture thickened, with weakly developed anterior and posterior siphons. Umbilicus narrow. Shell microstructure (Fig. 4) comprising four layers from external to internal: (1) irregular, simple prismatic structure, (2) simple radial crossed lamellar structure, (3) simple comarginal crossed lamellar structure, (4) irregular, simple prismatic structure.

External Anatomy: Operculum (Fig. 7) thin, transparent, light amber brown in color. Operculum spiral, comprising approximately six whorls, increasing evenly in size.

Foot narrowly ovate, with narrow propodium bearing shallow pedal gland along anterior margin (Fig. 6: ap). Columellar muscle extending to base of mantle cavity. In females, ovipositor (Fig. 6: ov) present on right side of foot, below eye, just behind foot sole margin. Aperture of ovipositor forming simple, oblique slit bounded by inflated folds; lumen



FIGS. 1–4. Shell morphology of *Bathania straeleni* (IRSNB no. 133, except when noted). FIG. 1: Adult shell. Scale bar = 5 mm; FIG. 2: Embryonic shell. Scale bar = 100 μ m; FIG. 3: Embryonic shell, apical view. Arrow indicates approximate transition to teleoconch. Scale bar = 100 μ m; FIG. 4: Shell microstructure (IRSNB no. 50). Cross section through shell parallel to aperture; outside of shell is uppermost. Order of layers from external to internal: (a) irregular, simple prismatic structure, (b) simple radial crossed lamellar structure, (c) simple comarginal crossed lamellar structure, (d) irregular, simple prismatic structure. Arrows indicate transitions between layers. Scale bar = 20 μ m.

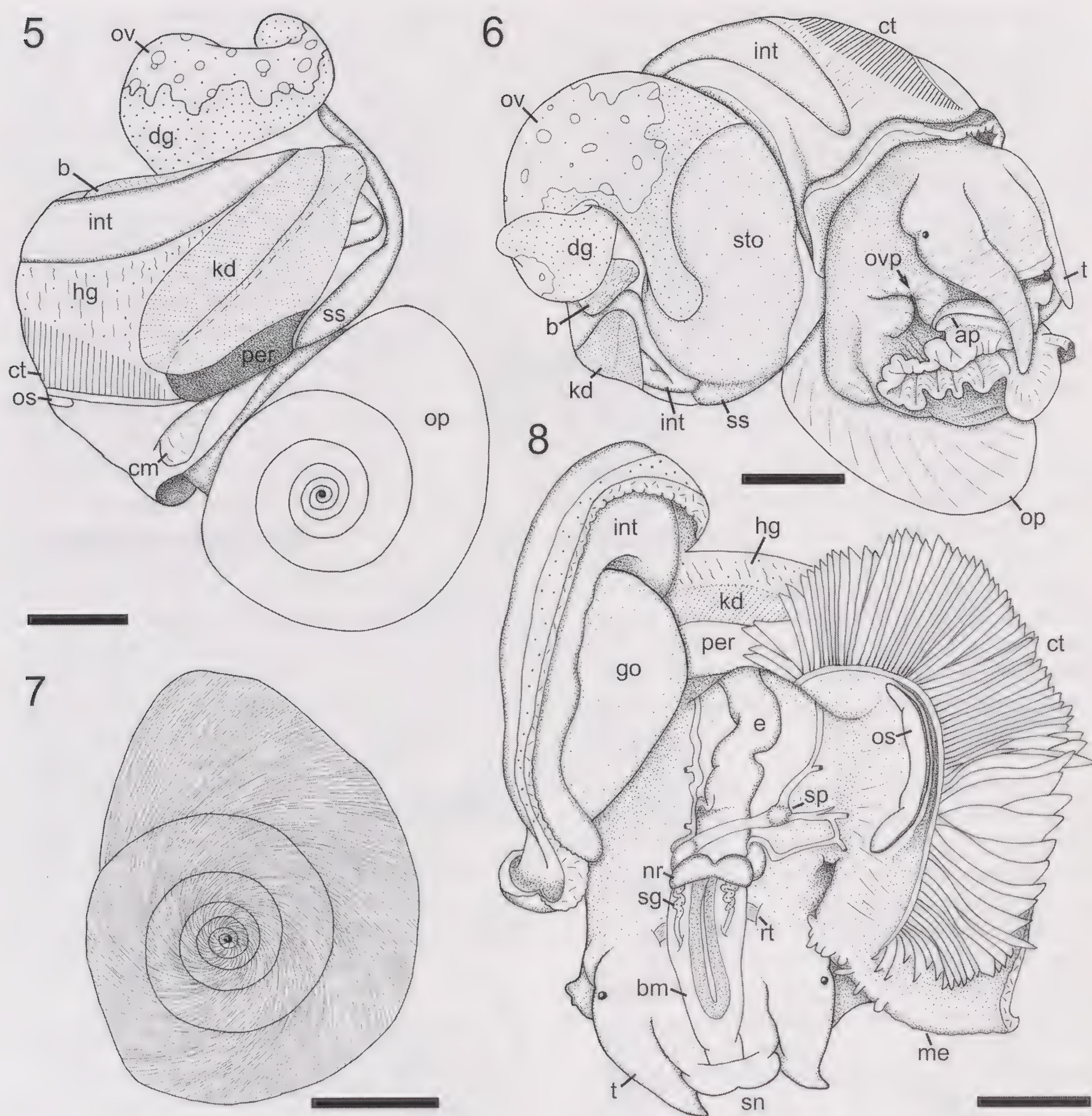
u-shaped with prominent fold projecting from floor. Finely grooved tract extending from pore, intersecting foot sole near anterior end of mesopodium. Ciliated egg groove between ovipositor and pallial oviduct lacking.

Retracted cephalic tentacles (Figs. 6, 8: t) smooth, short, thick, slightly longer than snout. Eyes located on small protuberances at base of tentacles. Snout (Fig. 8: sn) squarish, tapering to small mouth opening ventrally at tip.

Mantle cavity short, extending approximately one half whorl. Hypobranchial gland well developed (Figs. 5, 8: hg), thick, with

transverse grooves. Inhalant margin of mantle edge (Fig. 8: me) with ~8 small papillae. Ctenidium (Figs. 5, 6, 8: ct) extending from near mantle margin to rear of mantle cavity; leaflets narrowly triangular. Osphradium (Figs. 5, 8: os) smooth, short and thick, roughly one third of ctenidium in length, bordered by distinct ridge at left for most of length, becoming obsolete anteriorly.

Alimentary System: Foregut. Single specimen of radula was teratological and could not be used to make accurate observations on cusp

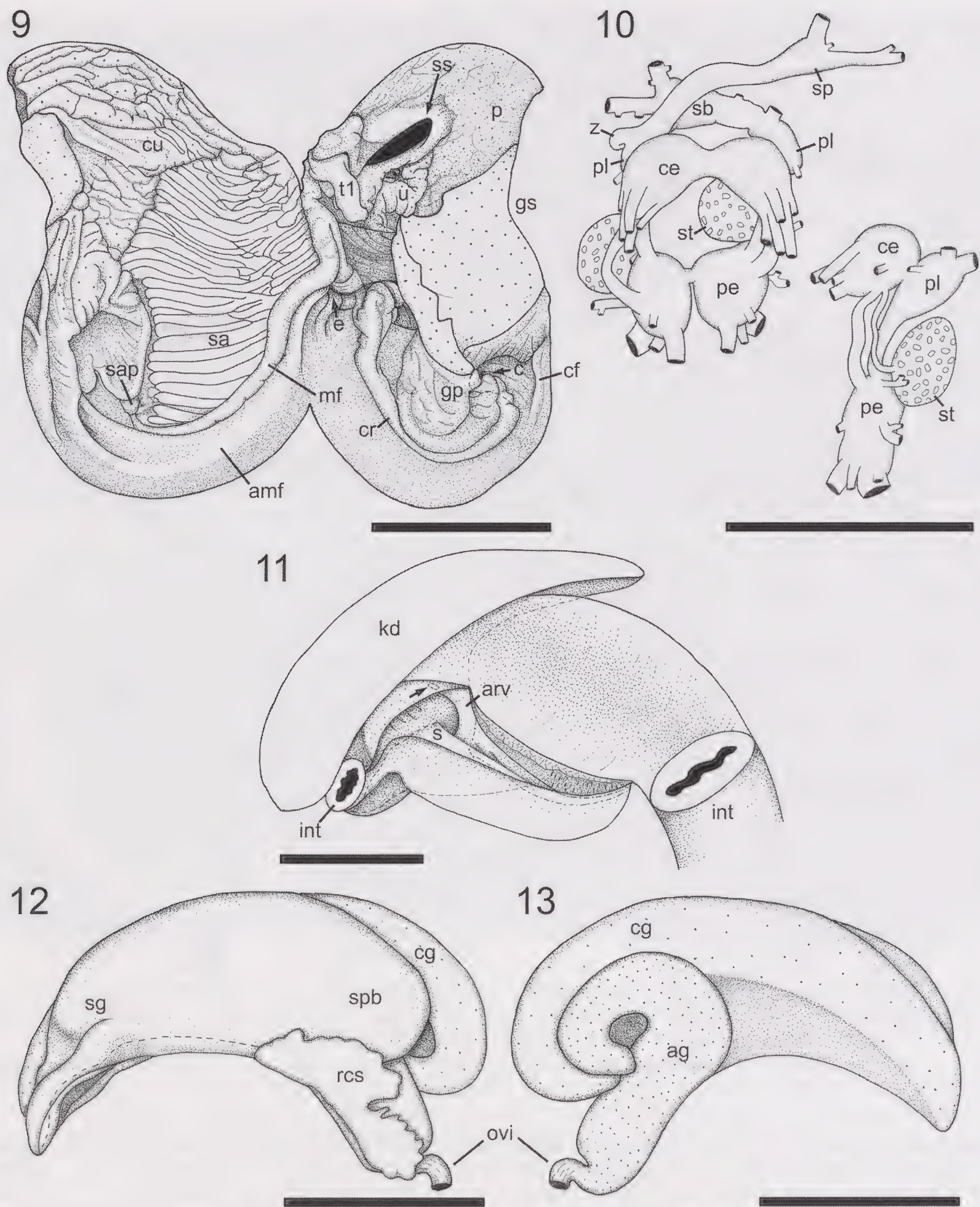


FIGS. 5–8. External anatomy of *Bathania straeleni* (IRSNB no. 50). FIG. 5: External view of organs in visceral mass. Dashed line indicates extent of pericardium under main kidney chamber; FIG. 6: External view of organs in visceral mass; right lateral view of female head-foot with ovipositor; FIG. 7: Operculum; FIG. 8: Dorsal view of mantle cavity and organs of cephalic hemocoel seen by transparency. Anterior is below. Abbreviations: ap, anterior pedal gland; b, bladder; bm, buccal mass; cm, columellar muscle; ct, ctenidium; dg, digestive gland; e, esophagus; go, pallial gonoduct; hg, hypobranchial gland; int, intestine; kd, kidney; me, mantle edge; nr, circumesophageal nerve ring; op, operculum; os, osphradium; ov, ovary; ovp, ovipositor; per, pericardium; rt, buccal retractor; sg, salivary gland; sn, snout; sp, supraesophageal ganglion; ss, style sac; sto, stomach; t cephalic tentacle. Scale bars = 1 mm.

morphology. Radula taenioglossate. Rachidian rectangular, roughly two times taller than wide, tapering to v-shaped lower margin. Upper margin slightly concave with cutting edge bearing prominent, central, sharply pointed cusp bounded by pointed denticles

on each side. Lateral teeth with extremely long lateral extensions, roughly twice as long as cutting edge. Marginal teeth with long, slender shafts.

Mouth opening ventrally at anterior end of snout. Buccal mass (Fig. 8: bm) narrow,



FIGS. 9–13. Internal anatomy of *Bathania straeleni* (IRSNB no. 50). FIG. 9: Midgut anatomy. Dorsal view, anterior is uppermost; FIG. 10: Circumesophageal nerve ring. Frontal view (above) and left lateral view (below); FIG. 11: Kidney anatomy. Internal view of bladder. Lateral view, anterior is at right. Roof of bladder (below intestine) cut open to reveal interior; FIG. 12: External, left lateral view of pallial oviduct. Anterior is at left. Single dashed line indicates free ventral edge of inner medial lamina wall, separating spermatophore bursa from gonoductal groove; FIG. 13: External, right lateral view of pallial oviduct. Anterior is at right. Abbreviations: ag, albumen gland; amf, accessory marginal fold; arv, afferent renal vessel; c, caecum; ce, cerebral ganglion; cf, caecal fold; cg, capsule gland; cr, crescentic ridge; cu, cuticularized region in midgut roof; e, esophagus; gp, glandular pad; gs, gastric shield; int, intestine; kd, kidney; mf, marginal fold; ovi, renal oviduct; p, crystalline style pocket; pe, pedal ganglion; pl, pleural ganglion; rcs, seminal receptacle; s, septum; sa, sorting area; sap, sorting area pad; sb, subesophageal ganglion; sg, seminal groove; sp, supraesophageal ganglion; spb, spermatophore bursa; ss, style sac; st, statocyst; t1, major typhlosole; u, u-shaped fold; z, zygoneury. Scale bars = 1 mm.

elongate; small odontophore occupying posterior half of buccal cavity. Narrowly triangular, glandular subradular organ extending along floor of buccal cavity at anterior end of odontophore. Small, paired jaw dorsally flanking mouth at anterior ends of dorsal folds. Shallow, nonglandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear of buccal cavity. Salivary glands (Fig. 8: sg) forming short, coiled, unbranched tubules, opening dorsolaterally alongside odontophore; salivary glands passing through circumesophageal nerve ring (Fig. 8: nr), but not extending posteriorly. Thick buccal retractors (Fig. 8: rt) extending from rear wall of buccal mass, inserting on lateral walls of cephalic hemocoel anterior to nerve ring. Nerve ring lying short distance back from posterior end of cephalic tentacles. Radular sac short, projecting slightly past end of buccal mass and curving dorsally underneath anterior esophagus. Within anterior esophagus, short, glandular midventral fold just behind odontophore. Paired ventral longitudinal folds commencing immediately behind midventral fold. Walls of anterior and midesophagus with paired, longitudinal ventral and dorsal folds and numerous additional, less prominent longitudinal grooves; dorsal and ventral folds fusing with each other (i.e., right dorsal fold with right ventral fold) at posterior end of midesophagus, enclosing shallow, weakly grooved, rear-projecting triangular troughs. Midesophageal gland lacking.

Midgut. Esophagus opening to gastric chamber floor at left (Fig. 9: e). Marginal fold (Fig. 9: mf) extending anteriorly alongside major typhlosole (Fig. 9: t1), then turning posteriorly bordering edge of sorting area (Fig. 9: sa). Sorting area rectangular, with rounded posterior margin. Marginal fold elaborated into small pad at left, posterior tip of sorting area (Fig. 9: sap). Accessory marginal fold (Fig. 9: amf) emerging from left side of esophageal aperture, paralleling marginal fold, curving anteriorly around posterior end of sorting area; accessory marginal fold bifurcate posteriorly. Epithelium of midgut floor finely grooved adjacent to major typhlosole at right of marginal fold. Midgut roof at left of sorting area deeply, irregularly creased, cuticularized (Fig. 9: cu). Gastric shield (Fig. 9: gs) large, continuous with cuticle of midgut roof and crystalline style pocket (Fig. 9: p). Broad, prominent fold bounding u-shaped depres-

sion (Fig. 9: u) below lip of style sac (Fig. 9: ss). Glandular pad (Fig. 9: gp) small, broadly rounded; accessory pad at anterior end lacking. Crescentic ridge (Fig. 9: cr) extending back from near esophageal aperture and fusing to right side of glandular pad, bounding shallow crescentic groove. Proximal tip of crescentic ridge bounding deep pouch with two digestive gland ducts. Shallow caecum (Fig. 9: c) extending ventrally under glandular pad behind gastric shield. Single, weakly developed longitudinal fold (Fig. 9: cf) behind gastric shield, opposite caecum. Style sac (Fig. 5: ss) communicating proximally with intestine. Crystalline style present.

Hindgut. Proximal intestine (Figs. 5, 6: int) passing below distal tip of style sac, then extending posteriorly alongside style sac (Figs. 5, 6: ss) to main gastric chamber (Fig. 6: sto). Intestine continuing forward, passing under posterior end of main kidney chamber (Figs. 5, 6: kd), entering pallial roof between bladder (Figs. 5, 6: b) and main kidney chamber, to papillate anus near mantle margin (Fig. 8: int).

Reno-Pericardial System: Voluminous kidney (Fig. 5: kd) extending from anterior end of main gastric chamber (Fig. 6: sto) alongside style sac and pericardium into mantle roof. Kidney lumen partially subdivided into two main chambers. Main chamber (Figs. 5, 11: kd) extending full length of kidney, surrounding pericardium dorsally and at right, anteriorly overhanging base of mantle cavity; lumen mostly occluded by excretory tubules developed in roof and along walls. Small bladder (Figs. 5, 6: b) at right of main chamber, extending into pallial roof between intestine (Fig. 5: int) and pallial gonoduct. Bladder (exposed chamber in Fig. 11) communicating with main chamber via small aperture (Fig. 11: arrow) just behind afferent renal vessel (Fig. 11: arv). Bladder partially subdivided posteriorly by incomplete horizontal septum of excretory tissue (Fig. 11: s), separating narrow triangular chamber below. Large sheet of excretory tubules branching from afferent renal vessel and extending anteriorly along bladder floor, partially separating narrow, shallow ventral chamber below. Nephridial gland absent.

Narrow, deep pericardium (Fig. 5: per) extending underneath kidney alongside style sac (Fig. 5: ss) past intestinal loop.

Nervous System: Cerebral ganglia (Fig. 10: ce) connected by short, stout commissure, each ganglion producing six nerves (optic, statocyst, tentacular, and three labial nerves). Buccal ganglia lying ventrolaterally at base of buccal mass, adjacent to retractor muscles, at outer edges of anterior esophagus. Pleural ganglia (Fig. 10: pl) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives. Pedal ganglia (Fig. 10: pe) with two prominent anterior nerves and approximately five smaller accessory nerves. Statocysts (Fig. 10: st) with numerous angular statoconia present dorsally alongside pedal ganglia behind pedal connectives. Subesophageal ganglion (Fig. 10: sb) joined to left pleural ganglion by long, thick connective; connective producing one small nerve. In addition to connectives to left pleural and visceral ganglia, subesophageal ganglion producing one stout, branching nerve, one fine nerve and zygoneurous connection to right pleural ganglion (Fig. 10: z). Long connective uniting right pleural and supraesophageal ganglia (Fig. 10: sp), the latter lying at left of midesophagus (Fig. 8: sp). Diallyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supraesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present at base of cephalic hemocoel.

Female Reproductive System: Gonad (Fig. 6: ov) dorsally overlying digestive gland (Fig. 6: dg) from tip of visceral mass to posterior end of gastric chamber (Fig. 6: sto). Oviduct emerging ventrally from ovary. Renal oviduct (Figs. 12, 13: ovi) forming short recurvent loop behind mantle cavity before entering base of glandular oviduct. Pallial oviduct, with proximal albumen (Fig. 13: ag) and distal capsule glands (Figs. 12, 13: cg). Albumen gland forming rear-facing c-shaped tube at posterior end of pallial oviduct; capsule gland developed along dorsal crest of pallial oviduct. Glandular tissue of capsule gland and much of albumen gland with opposing flattened surfaces bounding morphologically dorsal gonoductal groove. Lumen of albumen gland initially crescent-shaped, deepening abruptly just before broad, rear-facing loop. Narrow vagina along anterior one third of oviduct opening to sperm gutter (Fig. 12: sg) in median lamina. Gutter leading posteriorly to short, broad spermatophore bursa (Fig. 12: spb). Ventral free edge of median lamina inner wall (Fig. 12: dashed line) fusing

posteriorly above ventral channel, dorsally enclosing entrance to seminal receptacle (Fig. 12: rcs). Communication between sperm gutter and ventral channel bounded by two folds: one prominent dorsal fold along outer ventral edge of median lamina inner wall extending from anterior end of seminal groove to posterior end of bursa, dorsally bounding ventral channel, and one ventral shallow fold extending along ventral edge of vagina short distance along outer wall of bursa, to opening of seminal receptacle.

Male Reproductive System: Male reproductive anatomy unknown.

Remarks: The anatomy of *Bathanalia howesi* was described by Moore (1898) and found to be so similar to *Tiphobia* that he considered no special anatomical description necessary. Nevertheless, he felt that conchological differences were adequate to erect a separate genus. It should be emphasized that he did not explicitly confirm or reject that *B. howesi* was ovoviviparous; a figure of an animal removed from the shell (pl. 12, fig. 31) did not show a uterine brood pouch, but did not specify gender. Later, Moore (1903) reiterated the similarity with *Tiphobia*, but again was silent on the point of ovoviviparity. Moore (1898) made note of the diallyneury on the right that he managed to locate with the aid of histological sections, and which could not be located in *Tiphobia*; he considered this feature to be of special significance in assessing affinities of the two.

Through incorrect and incomplete descriptions of several anatomical features (including radula, midgut, and the nervous system in particular, erroneously described comprising a concentrated nerve ring and pedal cords with cross connections) and appalling misinterpretations of these structures seen through the lens of their "unquestionable" marine affinities (Moore, 1903), Moore (1898) placed *Tiphobia* and *Bathanalia* in their own family, the Tiphobiidae with affinities to the Stromboidea. He evidently was not aware that Bourguignat (1886) had already established this family-group name to circumscribe four species of *Tiphobia*, three of which are now considered synonyms of *Tiphobia horei*.

Leloup (1953: 132, fig. 72DD) figured a spiral operculum for *Bathanalia straeleni*, and reported a rachidian with 12/1/12; lateral teeth with 5–8/1/~15; almost identical marginal teeth with ~12/~15. Leloup (1953) also

reported that two juvenile shells (one empty and one containing an animal) had been recovered from the mantle cavity near the operculum of an individual of *B. straeleni* and concluded that this species is a uterine brooder. This observation, compounded by Moore's (1898) silence on this point, has formed the basis for a persistent misconception that *Bathanalia* species are ovoviviparous (e.g., Pilsbry & Bequaert, 1927; Brown, 1994; Glaubrecht, 2008). It is clear from examination of the figure in Leloup (1953: 135, fig. 73C) that the shell in question is not a juvenile *B. straeleni*, lacking the characteristic keel that develops rapidly in post-embryonic whorls (see Fig. 2), but rather is a juvenile of *Tiphobia horei* (Strong & Glaubrecht, 2007: fig. 8K, M), specimens of which were recovered from the same site (no. 50; Leloup, 1953). Consequently, the juveniles must have been drawn into the mantle cavity when the animal retracted. Female reproductive anatomy as revealed in the present investigation confirms that *B. straeleni* is not ovoviviparous as no embryos were recovered from the pallial oviduct of a sexually mature female, and the oviduct does not possess any characteristics commonly associated with uterine brooding (Strong & Glaubrecht, 2007).

Chytra kirkii
(Smith, 1880)

Material Examined: (BMNH 1880.12.21.11-14) (5 syntypes); (BMNH 1909.5.27.10-13) (4 spms); (BMNH, A.S. Kennard Colln., Acc. No. 1824) (3 spms); (BMNH) (4 spms); (BMNH 1953.8.15.248-257) (21 spms); (AMS 5493) (6 spms); (CM 62.29291) (3 spms); (DBL) (2 spms); (DBL) (1 spm); (USNM 120893) (1 spm); (USNM 149918) (1 spm); (ZMB 94.708) (4 spms); (ZMB 92.355) (3 spms). Burundi: Rumonge, 60 km S Bujumbura, 25–100 m (03°52'S, 29°23'E) (USNM 882005) (3 spms; 1 spm dissected). Democratic Republic of Congo: small bay to the south of Cape Tembwe (IRSNB no. 68) (1 spm). Tanzania: Malagarasi delta, 10–15 km from the coast, 33–17 m (IRSNB no. 63) (1 spm dissected); near Rusago (ZMB 220.155) (2 spms).

Shell: Adult shell comprising up to seven whorls, typically with broken apex (Fig. 14). Embryonic shell unknown. Teleoconch whorls flat, slightly rounded just below suture, with upturned basal keel just above suture. Teleoconch axial sculpture comprising fine sig-

moidal growth lines. Early teleoconch whorls smooth, rapidly developing two fine spiral cords, soon joined by two additional spiral cords, plus one spiral cord along basal keel. Cords thickening and becoming nodulose. Single fine spiral thread appearing between each of initial four cords; spiral threads thickening and becoming nodulose on later adult teleoconch whorls. Growth lines becoming more prominent on final teleoconch whorl. Basal disk of shell sculptured with numerous, prominent nodulose spiral cords. Aperture thickened, angular but holostome. Umbilicus narrow. Shell microstructure (Fig. 15) comprising five layers from external to internal: (1) irregular, simple prismatic structure, (2) simple radial crossed lamellar structure, (3) simple comarginal crossed lamellar structure, (4) simple radial crossed lamellar structure, (5) irregular, simple prismatic structure.

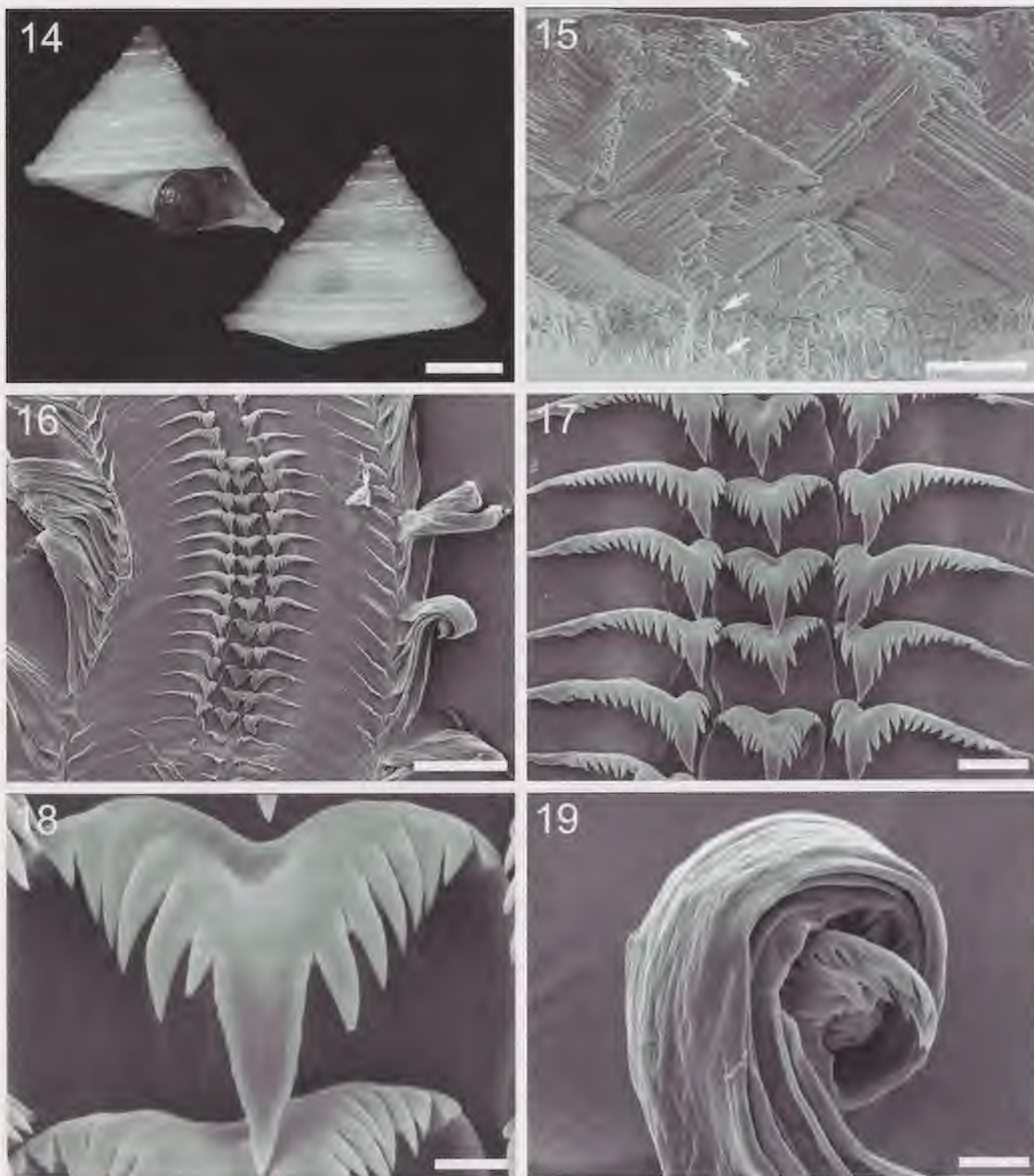
External Anatomy: Operculum (Fig. 21) transparent, amber brown in color. Operculum spiral, comprising approximately 5.5 whorls, increasing evenly in size.

Foot narrowly ovate, with narrow propodium with shallow pedal gland along anterior margin (Fig. 23: ap). Columellar muscle extending to anterior end of style sac, just behind base of mantle cavity. In females, ovipositor present (Fig. 20: ov) on right side of foot, just behind foot sole margin at junction of propodium and mesopodium. Aperture of ovipositor forming simple, oblique slit bounded by inflated folds; lumen shallow, simple, with fine grooves. Finely grooved tract to foot sole and ciliated egg groove between ovipositor and pallial oviduct both lacking.

Cephalic tentacles (Figs. 20, 23: t) smooth, long, tapering, more than twice as long as snout. Eyes located on small protuberances at base of tentacles. Snout rounded, tapering anteriorly to small mouth opening at tip.

Mantle cavity short, extending approximately one half whorl. Hypobranchial gland thin, inconspicuous (Fig. 22: hg). Mantle edge smooth. Ctenidium (Figs. 22, 23: ct) extending from near mantle margin to rear of mantle cavity; leaflets narrowly triangular. Osphradium (Fig. 23: os) smooth, short, roughly one fourth of ctenidium in length, bordered by distinct ridge at right for most of length, and at left by overhanging efferent branchial vessel.

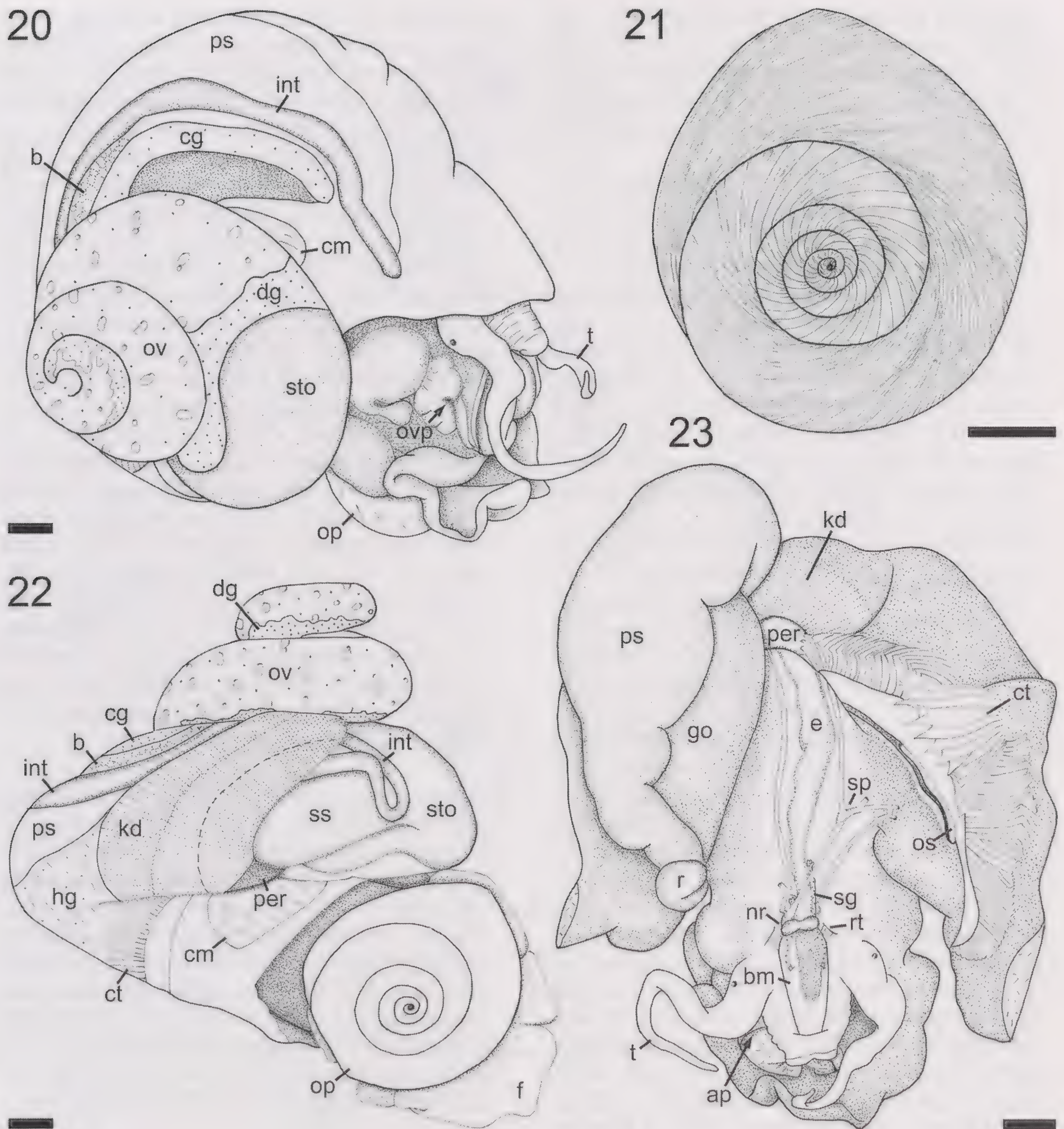
Alimentary System: *Foregut.* Radula taenioglossate (Fig. 16). Rachidian (Fig. 17) squar-



FIGS. 14–19. Shell and radula morphology of *Chytra kirkii* (IRSNB no. 63, except when noted). FIG. 14: Adult shell (IRSNB no. 68). Scale bar = 5 mm; FIG. 15: Shell microstructure. Cross section through shell parallel to aperture; outside of shell is uppermost. Order of layers from external to internal: (a) irregular, simple prismatic structure, (b) simple radial crossed lamellar structure, (c) simple comarginal crossed lamellar structure, (d) simple radial crossed lamellar structure, (e) irregular, simple prismatic structure. Arrows indicate transitions between layers. Scale bar = 50 μ m; FIG. 16: Radula. Scale bar = 100 μ m; FIG. 17: Rachidian and lateral teeth. Scale bar = 20 μ m; FIG. 18: Rachidian tooth. Scale bar = 5 μ m; FIG. 19: Marginal teeth. Scale bar = 10 μ m.

ish, tapering to v-shaped lower margin. Upper margin slightly concave, with cutting edge bearing single, prominent, pointed central

cuspid bounded by six to eight pointed denticles on each side (Fig. 18). Lateral teeth with extremely long lateral extensions (Fig. 16),



FIGS. 20–23. External anatomy of *Chytra kirkii* (IRSNB no. 63). FIG. 20: External view of organs in visceral mass; right lateral view of female head-foot with ovipositor; FIG. 21: Operculum; FIG. 22: External view of organs in visceral mass. Dashed line indicates extent of pericardium under main kidney chamber; FIG. 23: Dorsal view of mantle cavity and organs of cephalic hemocoel seen by transparency. Anterior is below. Abbreviations: ap, anterior pedal gland; b, bladder; bm, buccal mass; cg, capsule gland; cm, columellar muscle; ct, ctenidium; dg, digestive gland; e, esophagus; f, foot; go, pallial gonoduct; hg, hypobranchial gland; int, intestine; kd, kidney; nr, circumesophageal nerve ring; op, operculum; os, osphradium; ov, ovary; per, pericardium; ovp, ovipositor; ps, periintestinal sinus; r, rectum; rt, buccal retractor; sg, salivary gland; sp, supraesophageal ganglion; ss, style sac; sto, stomach; t cephalic tentacle. Scale bars = 1 mm.

roughly twice as long as cutting edge. Cutting edge with single, prominent pointed cusp flanked by five to seven inner and 9–14 outer pointed denticles. Outermost denticles of lat-

eral teeth often fused and forming undulating, overhanging ridge. Marginal teeth (Figs. 16, 19) long, slender, with narrow, spoon-shaped tips bearing fine, pointed denticles of similar

size and shape; inner marginal teeth with roughly five denticles, outer marginal teeth with roughly 8 denticles along inner edge. Precise dentition of marginal teeth could not be assessed due to curling and clumping of teeth of single available specimen.

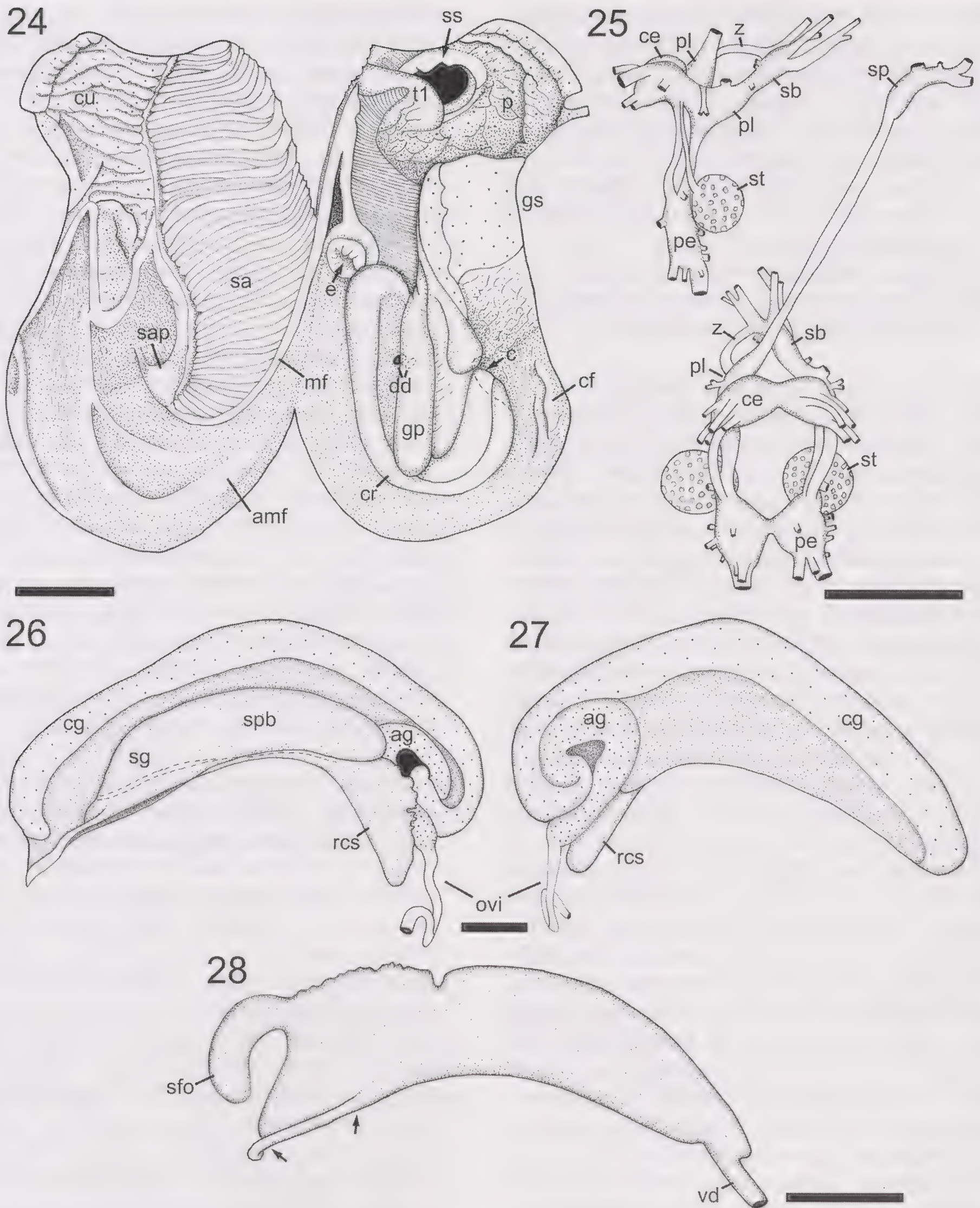
Mouth opening ventrally at anterior end of snout. Buccal mass (Fig. 23: bm) narrow, elongate; small odontophore occupying posterior half of buccal cavity. Narrowly triangular, glandular subradular organ extending along floor of buccal cavity at anterior end of odontophore. Small, paired jaw dorsally flanking mouth at anterior ends of dorsal folds. Shallow, nonglandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear of buccal cavity. Salivary glands (Fig. 23: sg) forming short, coiled tubules with branching tips, opening dorsolaterally alongside odontophore; salivary glands passing through circumesophageal nerve ring (Fig. 23: nr). Salivary glands asymmetrical with right gland terminating within nerve ring and left gland extending short distance posteriorly. Thick buccal retractors (Fig. 23: rt) extending from rear wall of buccal mass, inserting on lateral walls of cephalic hemo-coel alongside nerve ring. Nerve ring lying short distance back from posterior end of cephalic tentacles. Radular sac short, projecting slightly past end of buccal mass and curving dorsally underneath anterior esophagus. Within anterior esophagus, short, glandular midventral fold just behind odontophore. Paired ventral longitudinal folds commencing immediately behind midventral fold. In single well-preserved specimen, ventral folds apparently fusing for short distance at anterior end of midesophagus and forming elevated, transverse fold, then separating and continuing through midesophagus. Walls of anterior and midesophagus with paired, longitudinal ventral and dorsal folds; dorsal and ventral folds continuing through midesophagus and continuous with folds in posterior esophagus. Posterior esophagus with numerous folds of equal height. Midesophageal gland lacking.

Midgut. Esophagus opening to gastric chamber floor at left (Fig. 24: e). Marginal fold (Fig. 24: mf) extending anteriorly alongside major typhlosole (Fig. 24: t1), then turning posteriorly bordering edge of sorting area (Fig. 24: sa). Sorting area rectangular, with rounded posterior margin. Marginal fold elaborated into small, flattened pad at left, posterior tip of sorting area (Fig. 24: sap). Accessory

marginal fold (Fig. 24: amf) emerging from left side of esophageal aperture, paralleling marginal fold, curving anteriorly around posterior end of sorting area; accessory marginal fold bifurcate posteriorly. Epithelium of midgut floor finely, regularly grooved at right of marginal fold and along projecting tip of major typhlosole. Anterior midgut roof at left of sorting area deeply, irregularly creased, cuticularized (Fig. 24: cu). Gastric shield (Fig. 24: gs) moderately large, continuous with cuticle of midgut roof and crystalline style pocket (Fig. 24: p). Glandular pad (Fig. 24: gp) large, elongate, broadly rounded; accessory pad at anterior end lacking. Crescentic ridge (Fig. 24: cr) extending back from near esophageal aperture and fusing to right side of glandular pad, bounding deep, narrow crescentic groove. Proximal crescentic ridge bounding two digestive gland ducts at left (Fig. 24: dd). Very shallow caecum (Fig. 24: c) extending ventrally under glandular pad behind gastric shield. One to two weakly developed longitudinal folds (Fig. 24: cf) behind gastric shield, opposite caecum. Style sac (Fig. 22: ss) communicating proximally with intestine). Crystalline style present.

Hindgut. Proximal intestine (Fig. 22: int) passing below distal tip of style sac, then extending posteriorly alongside style sac (Fig. 22: ss), forming broad loop over proximal style sac adjacent to main gastric chamber (Fig. 22: sto). Intestine continuing forward, passing under posterior end of main kidney chamber (Fig. 22: kd), entering pallial roof between bladder (Fig. 22: b) and main kidney chamber, to papillate anus near mantle margin (Fig. 23: r). Voluminous periintestinal sinus (Fig. 23: ps) surrounding pallial portion of intestine.

Reno-Pericardial System: Voluminous kidney (Fig. 22: kd) extending from anterior end of main gastric chamber (Fig. 22: sto) alongside style sac and pericardium into mantle roof. Kidney lumen partially subdivided into two main chambers. Main chamber (Fig. 20: kd) extending full length of kidney, surrounding pericardium dorsally and at right, anteriorly overhanging base of mantle cavity; lumen mostly occluded by excretory tubules developed in roof and along walls. Large bladder (Figs. 20, 22: b) at right of main chamber, extending into pallial roof between intestine (Figs. 20, 22: int) and pallial gonoduct (Figs. 20, 22: cg). Bladder communicating with main chamber via small aperture just behind affer-



FIGS. 24–28. Internal anatomy of *Chytra kirkii* (IRSNB no. 63, except when noted). FIG. 24: Midgut anatomy. Dorsal view, anterior is uppermost; FIG. 25: Circumesophageal nerve ring. Left lateral view (above) and frontal view (below); FIG. 26: External, left lateral view of pallial oviduct. Anterior is at left. Double dashed line indicates opening from bursa to gonoductal groove; single dashed line indicates continuation of inner edge of medial lamina as shallow groove to opening of seminal receptacle; FIG. 27: External, right lateral view of pallial oviduct. Anterior is at right; FIG. 28: External, left lateral view of prostate (USNM 882005). Anterior is at left. Arrows indicate extent of opening to gonoductal groove. Prominent grooves of lateral lamina seen by transparency. Abbreviations: ag, albumen gland; amf, accessory marginal fold; c, caecum; ce, cerebral ganglion; cf, caecal fold; cg, capsule gland; cr, crescentic ridge; cu, cuticularized region in midgut roof; dd, digestive gland duct; e, esophagus; gp, glandular pad; gs, gastric shield; mf, marginal fold; ovi, renal oviduct; p, crystalline style pocket; pe, pedal ganglion; pl, pleural ganglion; rcs, seminal receptacle; sa, sorting area; sb, subesophageal ganglion; sap, sorting area pad; sfo, spermatophore forming organ; sg, seminal groove; sp, supraesophageal ganglion; spb, spermatophore bursa; ss, style sac; st, statocyst; t1, major typhlosole; vd, vas deferens; z, zygoneury. Scale bars = 1 mm.

ent renal vessel. Bladder partially subdivided posteriorly by incomplete horizontal septum of excretory tissue, separating short, broad chamber below. Large sheet of excretory tubules branching from afferent renal vessel and extending anteriorly along bladder floor. Excretory tissue in bladder highly developed along floor and roof, mostly occluding lumen. Nephridial gland absent.

Narrow, deep pericardium (Fig. 22: per) extending underneath kidney alongside style sac (Fig. 22: ss) to intestinal loop.

Nervous System: Cerebral ganglia (Fig. 25: ce) connected by short, stout commissure, each ganglion producing six nerves (optic, statocyst, tentacular, and three labial nerves). Buccal ganglia lying ventrolaterally at base of buccal mass, at inner edge of retractor muscles, below anterior esophagus. Pleural ganglia (Fig. 25: pl) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives. Pedal ganglia (Fig. 25: pe) with two prominent anterior nerves and approximately seven to eight smaller accessory nerves. Statocysts (Fig. 25: st) with numerous angular statoconia present dorsally alongside pedal ganglia behind pedal connectives. Subesophageal ganglion (Fig. 25: sb) joined to left pleural ganglion by long, thick connective; connective producing one small nerve. In addition to connectives to left pleural and visceral ganglia, subesophageal ganglion producing one stout, branching nerve, one finer branching nerve, two small accessory nerves and zygoneurous connection to right pleural ganglion (Fig. 25: z). Very long connective uniting right pleural and supraesophageal ganglia (Fig. 25: sp), the latter lying at left of cephalic hemocoel, well back from circumesophageal nerve ring (Fig. 23: sp). Diallyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supraesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present at base of cephalic hemocoel.

Female Reproductive System: Gonad (Fig. 20: ov) dorsally overlying digestive gland (Fig. 20: dg) from tip of visceral mass to posterior end of gastric chamber (Fig. 20: sto). Oviduct emerging ventrally from ovary. Renal oviduct (Figs. 26, 27: ovi) forming short recurvent loop behind mantle cavity before entering base of glandular oviduct. Pallial oviduct, with proximal albumen (Figs. 26, 27: ag) and

distal capsule glands (Figs. 26, 27: cg). Albumen gland forming rear-facing c-shaped tube at posterior end of pallial oviduct; capsule gland developed along dorsal crest of pallial oviduct. Glandular tissue of capsule gland and much of albumen gland with opposing flattened surfaces bounding morphologically dorsal gonoductal groove. Lumen of albumen gland initially crescent-shaped, deepening abruptly just before broad, rear-facing loop. Narrow vagina along anterior one third of oviduct opening to sperm gutter (Fig. 26: sg) in median lamina. Gutter leading posteriorly to elongate, narrow spermatophore bursa (Fig. 26: spb). Inner wall of median lamina fusing to outer wall, restricting communication between spermatophore bursa and ventral channel to short, anterior slit (Fig. 26: double dashed line). Ventral edge of median lamina inner wall (Fig. 26: single dashed line) continuing posteriorly as shallow groove above ventral channel, posteriorly enclosing entrance to seminal receptacle (Fig. 26: rcs). Communication between sperm gutter and ventral channel bounded by shallow fold extending along ventral edge of vagina.

Male Reproductive System: Single immature specimen available. Narrow vas deferens (Fig. 28: vd) emerging ventrally from testes, entering posterior end of prostate at base of mantle cavity. Prostate glandular, forming flattened tube, opening to mantle cavity through narrow, ventral slit along anterior one fourth to one fifth (arrows). Posterior two thirds of prostate separated from anterior third by slight dorsal constriction. Glands of posterior lateral lamina dorsally deeply longitudinally grooved; anterior portion of lateral lamina with deep oblique trough extending ventrally from dorsal constriction to above anterior end of aperture. Posterior medial lamina more weakly and irregularly longitudinally grooved; anterior medial lamina rather smooth with oblique, rear facing fine grooves along dorsal undulating ridge. Dorsal, anterior portion of prostate forming short, glandular, tube-like spermatophore-forming organ (Fig. 28: sfo). Organ terminating blindly anteriorly, communicating posteriorly with gonoductal groove via narrow aperture.

Remarks: The anatomy was described by Digby (1902), who provided accurate if not detailed descriptions of the operculum, mantle cavity (with short osphradium), radula (with considerably more denticles on the mar-

ginal teeth), midgut (with crescentic ridge and glandular pad interpreted as a spiral caecum), and nervous system (with dialyneury on the left, and zygoneury on the right, statocysts with numerous statoconia). As was typical of the time, female reproductive anatomy was described simply as a uterus. It is likely that Digby (1902) misinterpreted male reproductive anatomy for female, given the similarity of a putatively female pallial gonoduct (pl. 39, fig. 12) to a male prostate with spermatophore forming organ (as “accessory genital gland”). Digby (1902) concluded the species to be an ancestor of the Hipponicidae and Capulidae. Moore (1903) reproduced parts of Digby’s (1902) description, and featured an operculum and one row of the radula.

Leloup figured (1953: 132, fig. 72Z) a spiral operculum, and reported the radula with a rachidian broader than tall, with 7–13/1/7–13; lateral teeth with 3–5/1/10–13; similar marginal teeth with 12–19/9–15. Riedel (1993) provided a description of the embryonic shell, including SEM micrographs (fig. 22; pl. 4, figs. 7, 8), showing the great similarity with the embryonic shell of *Limnotrochus* (Figs. 30–32); the two differing primarily in the ornament of the early teleoconch. West & Cohen (1996) reported four layers of crossed lamellar microstructure in the shell.

Limnotrochus thomsoni
Smith, 1880

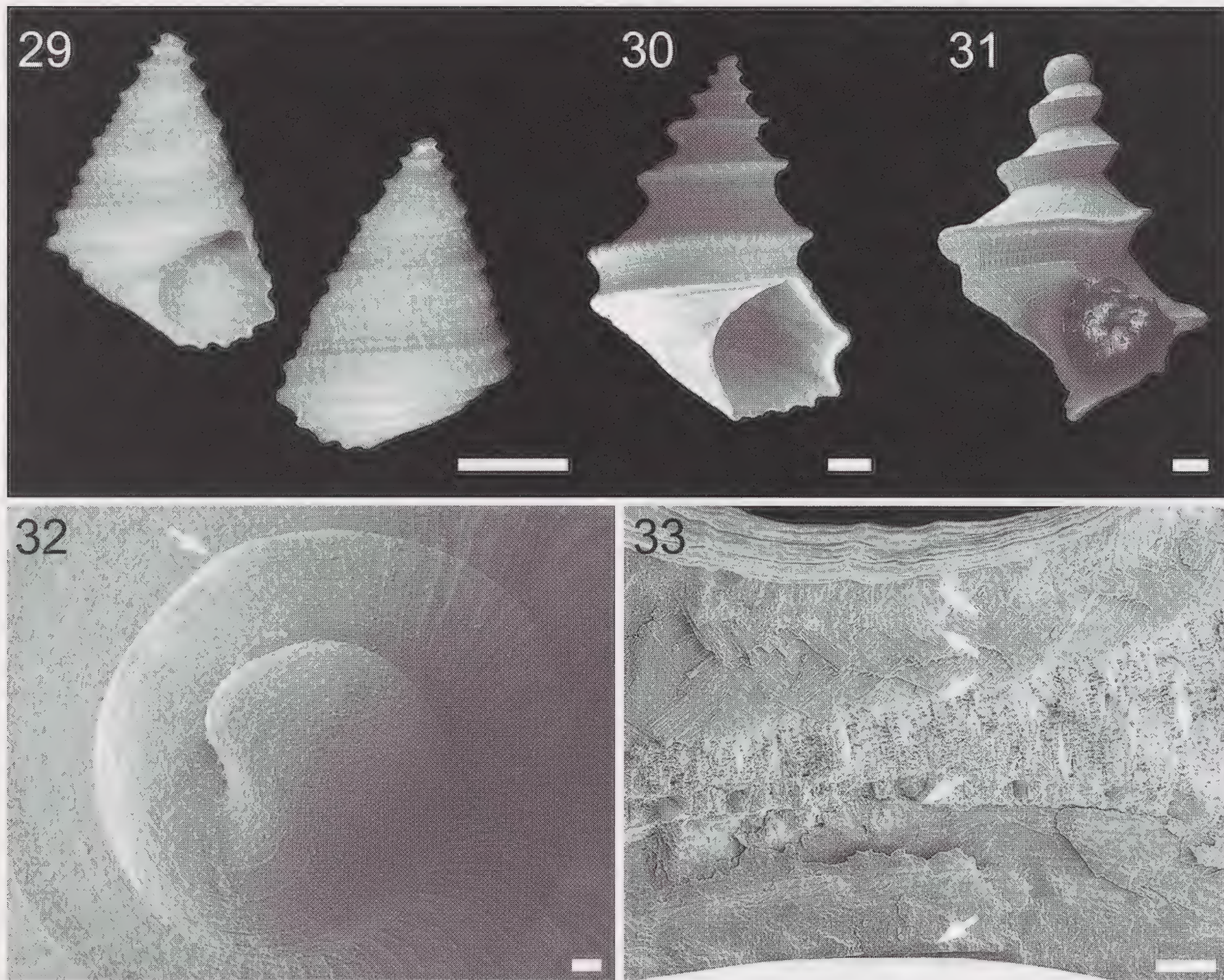
Material Examined: (BMNH 1880.12.20.45–8) (4 syntypes); (AMS C.5492) (3 spms); (BMNH, A.S. Kennard Colln., Acc. No. 1824) (2 spms); (BMNH 89.6.3.20–1) (3 spms); (BMNH 1953.8.15.235–37) (3 spms); (NHMB 830a) (18 spms); (NHMB 830b) (2 spms); (USNM 127173) (2 spms); ZMB 35243 (2 spms); ZMB 220.162 (2 spms); (MRAC) (3 spms); (ZMB 35243). Burundi: Rumonge, 60 km S Bujumbura, 25–100 m (03°52’S, 29°23’E) (USNM 882015) (6 spms); Nyanza-Lac, 35–40 ft (04°20’S, 29°36’E) (USNM 857904) (1 spm). Democratic Republic of Congo: (DBL) (1 spm); Kalemie (BMNH) (2 spms); same (USNM 341838) (1 spm). Tanzania: beach S of Karema (ZMB 220.031) (3 spms); Kigoma (BMNH 1920.10.26.199) (1 spm); near Rusago (ZMB 220.032) (1 spm); Uva Island, near Kassanga (ZMB 52268) (1 spm). Zambia: Chipata Bay, 80 m (08°41.700’S, 31°08.952’E) (ZMB 220.162) (2 spms); Kasakalawe, 4–5 m (08°47.480’S, 31°04.494’E) (ZMB 220.087) (2 spms); Ka-

senga Point, 2 m (08°42.887’S, 31°08.476’E) (ZMB 220.025) (1 spm); Kombe (08°47.52’S, 31°01.11’E) (ZMB 107.056) (1 spm); same (ZMB 107.057) (1 spm); same (ZMB 107.058) (1 spm); same (ZMB 107.059) (1 spm); same (ZMB 107.060) (1 spm dissected); same (ZMB 107.102) (9 spms); Kumbula Island, 21 m (08°45.258’S, 31°05.116’E) (ZMB 220.038) (1 spm dissected); Mpulungu Field Station, 6 m (08°45.992’S, 31°06.402’E) (ZMB 220.065) (2 spms; 1 spm dissected); Mpulungu (DBL) (2 spms); same, 30 m (DBL) (6 spms).

Shell: Adult shell comprising up to six whorls, typically with broken apex (Fig. 29). Apical cap of embryonic shell with irregularly, finely textured surface, rapidly giving way to numerous fine spiral threads (Fig. 32). Gradual transition to teleoconch marked by development of smooth, sigmoidally curved, opisthocyrt axial threads, undulating peripheral keel at shoulder and prominent spiral cord below keel at suture (Fig. 31). By third teleoconch whorl, spiral threads becoming obsolete and one additional spiral cord appearing between keel and basal cord, visible on flattened basal portion of whorl. By sixth teleoconch whorl, additional spiral threads appearing, producing reticulate pattern on upper portion and sides of whorl; three to four prominent cords appearing on basal portion of whorl producing undulating lower surface (Fig. 30). By sixth whorl, keel developing nodulose sculpture. On subsequent teleoconch whorls, three nodulose cords appearing above keel, appearing in order from most prominent below suture, to least prominent just above keel; cord at suture and cords on base becoming nodulose. Aperture thickened, with weakly developed posterior siphon. Umbilicus narrow. Shell microstructure (Fig. 33) comprising six layers from external to internal: (1) irregular, simple prismatic structure, (2) simple radial crossed lamellar structure, (3) simple comarginal crossed lamellar structure, (4) simple radial crossed lamellar structure, (5) irregular, complex crossed lamellar structure, (6) irregular, simple prismatic structure.

External Anatomy: Operculum (Fig. 35) transparent, amber brown in color. Operculum weakly paucispiral, comprising approximately 4.5 whorls. Initial four whorls increasing gradually in diameter; final one half whorl expanding rapidly, increasing roughly twice in diameter.

Foot narrowly ovate, with narrow propodium bearing shallow pedal gland along anterior



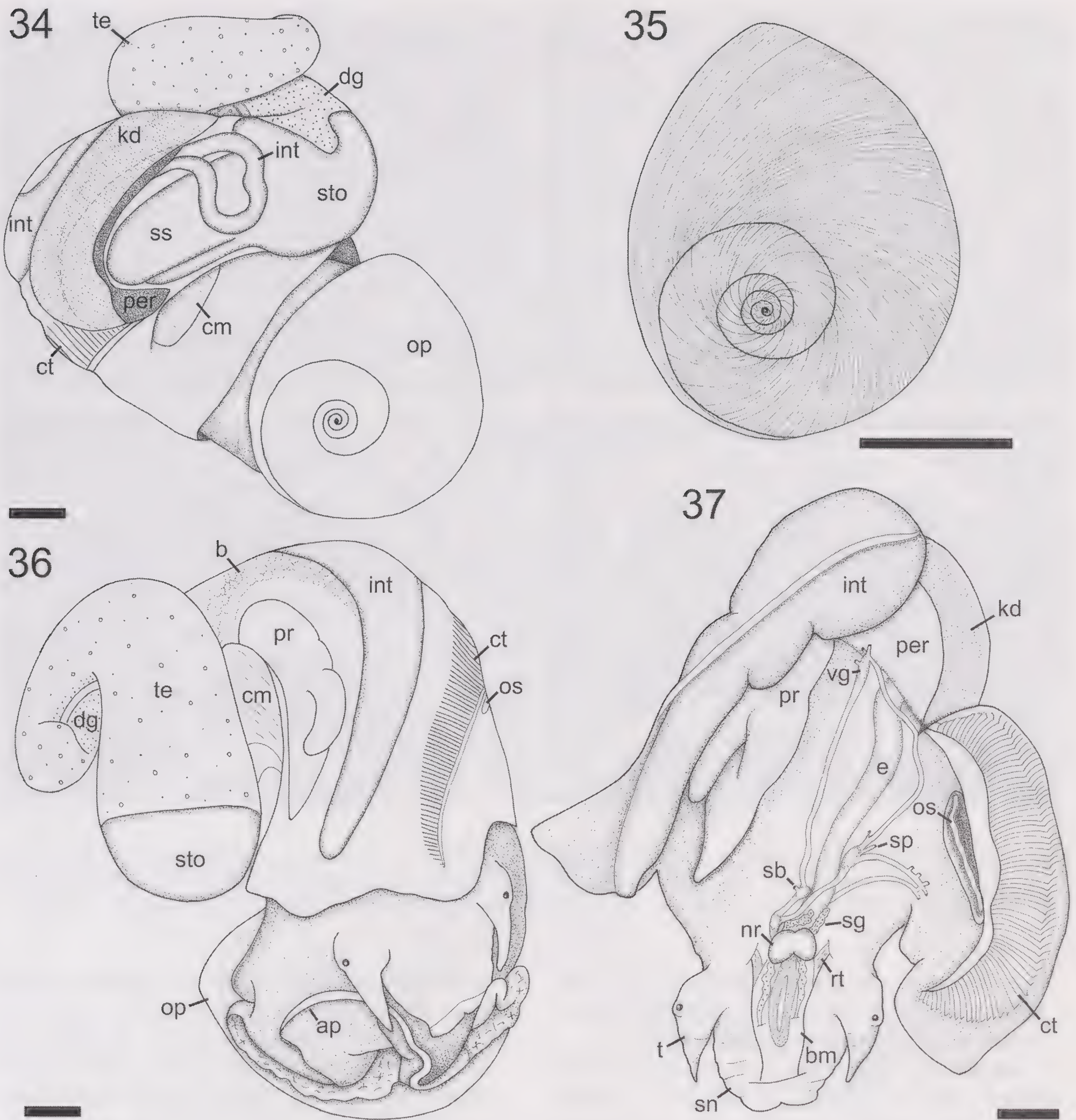
FIGS. 29–33. Shell morphology of *Limnotrochus thomsoni*. FIG. 29: Adult shell (ZMB 107.102). Scale bar = 5 mm; FIG. 30: Shell of sub-adult (DBL). Scale bar = 1 mm; FIG. 31: Juvenile shell (DBL). Scale bar = 200 μ m; FIG. 32: Embryonic shell (DBL), apical view. Arrow indicates approximate transition to teleoconch. Scale bar = 20 μ m; FIG. 33: Shell microstructure (ZMB 220.038). Cross section through shell parallel to aperture; outside of shell is uppermost. Order of layers from external to internal: (a) irregular, simple prismatic structure, (b) simple radial crossed lamellar structure, (c) simple comarginal crossed lamellar structure, (d) simple radial crossed lamellar structure, (e) irregular, complex crossed lamellar structure, (f) irregular, simple prismatic structure. Arrows indicate transitions between layers. Scale bar = 100 μ m.

margin (Fig. 36: ap). Columellar muscle extending to style sac, just behind base of mantle cavity. In females, ovipositor present on right side of foot, just behind foot sole margin at junction of propodium and mesopodium. Aperture of ovipositor forming simple, oblique slit bounded by low folds; lumen shallow, simple. Finely grooved tract to foot sole and ciliated egg groove between ovipositor and pallial oviduct both lacking.

Cephalic tentacles (Fig. 37: t) smooth, short, triangular, slightly less than snout in length. Eyes located on small protuberances at base of tentacles. Snout rounded, tapering anteriorly to small mouth opening at tip.

Mantle cavity short, extending approximately one half whorl. Hypobranchial gland thin, inconspicuous. Mantle edge smooth. Ctenidium (Figs. 34, 36, 37: ct) extending from near mantle margin to rear of mantle cavity; leaflets broadly triangular. Osphradium (Figs. 36, 37: os) smooth, short, roughly one third of ctenidium in length, bordered by distinct ridge at right for most of length, and at left by overhanging efferent branchial vessel.

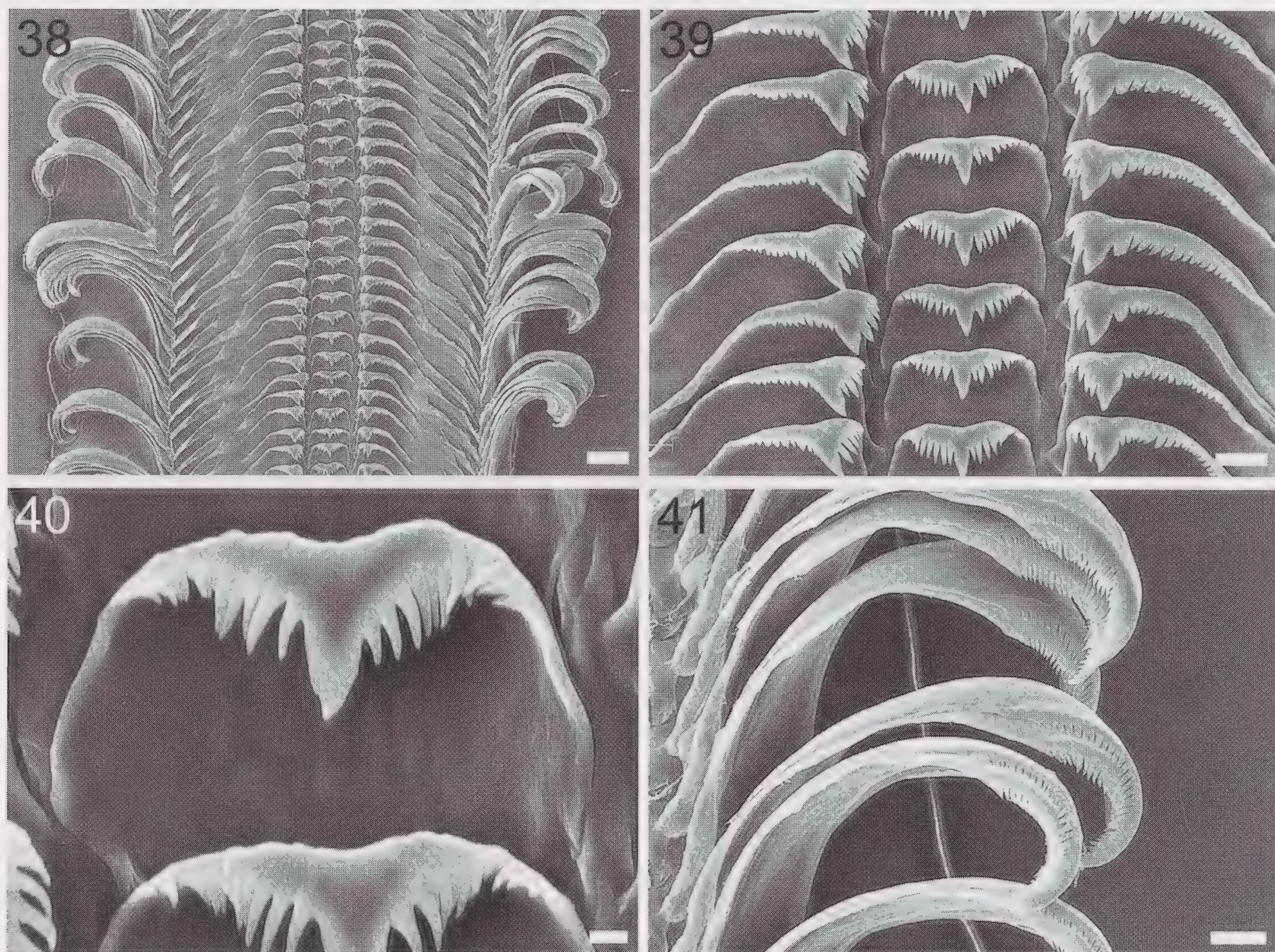
Alimentary System: Foregut. Radula taenioglossate (Fig. 38). Rachidian (Fig. 39) rectangular, wider than tall, tapering to v-



FIGS. 34–37. External anatomy of *Limnotrochus thomsoni* (ZMB 220.065). FIG. 34: External view of organs in visceral mass. Dashed line indicates extent of pericardium under main kidney chamber; FIG. 35: Operculum; FIG. 36: External view of organs in visceral mass; FIG. 37: Dorsal view of mantle cavity and organs of cephalic hemocoel seen by transparency. Anterior is below. Abbreviations: ap, anterior pedal gland; b, bladder; bm, buccal mass; cm, columellar muscle; ct, ctenidium; dg, digestive gland; e, esophagus; int, intestine; kd, kidney; nr, circumesophageal nerve ring; op, operculum; os, osphradium; per, pericardium; pr, prostate; rt, buccal retractor; sb, subesophageal ganglion; sg, salivary gland; sn, snout; sp, supraesophageal ganglion; ss, style sac; sto, stomach; t cephalic tentacle; te, testis; vg, visceral ganglion. Scale bars = 1 mm.

shaped lower margin. Upper margin slightly concave, with cutting edge bearing single, prominent, pointed central cusp bounded by 9–13 fine, pointed denticles on each side (Fig. 40). Lateral teeth with extremely long lateral extensions (Fig. 38), roughly twice

as long as cutting edge. Cutting edge with single, prominent pointed cusp flanked by six to seven inner and 16–20 outer pointed denticles. Outermost denticles of lateral teeth often fused and forming undulating, overhanging ridge. Marginal teeth (Figs. 38, 41)



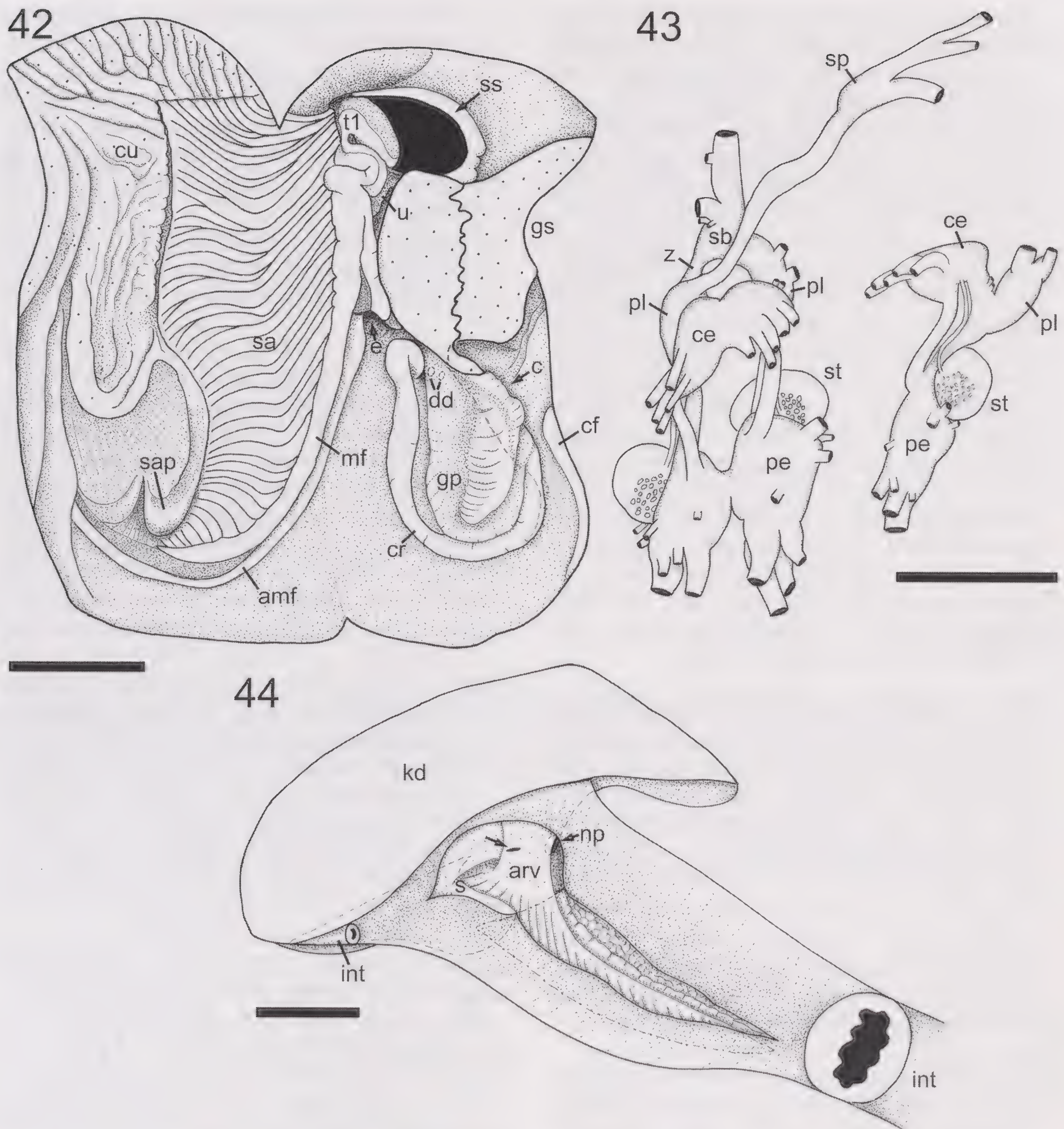
FIGS. 38–41. Radula morphology of *Limnotrochus thomsoni*. FIG. 38: Radula (ZMB 220.038). Scale bar = 30 μ m; FIG. 39: Rachidian and lateral teeth (ZMB 220.038). Scale bar = 10 μ m; FIG. 40: Rachidian tooth (ZMB 220.038). Scale bar = 2 μ m; FIG. 41: Marginal teeth (ZMB 220.038). Scale bar = 10 μ m.

long, slender, with narrow, elongate, rounded tips bearing ~28–32 fine, pointed denticles of similar size and shape along inner edge.

Mouth opening ventrally at anterior end of snout. Buccal mass (Fig. 37: bm) narrow, elongate; small odontophore occupying posterior half of buccal cavity. Narrowly triangular, glandular subradular organ extending along floor of buccal cavity at anterior end of odontophore. Small, paired jaw dorsally flanking mouth at anterior ends of dorsal folds. Shallow, nonglandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear of buccal cavity. Salivary glands (Fig. 37: sg) forming long, highly convoluted tubules with grape-like branching tips, opening dorsolaterally alongside odontophore; salivary glands passing through circumesophageal nerve ring (Fig. 37: nr) and extending short distance posteriorly. Thick buccal retractors (Fig. 37: rt) extending from rear wall of buccal mass,

inserting on lateral walls of cephalic hemo-coel alongside nerve ring. Nerve ring lying near base of cephalic tentacles. Radular sac short, projecting slightly past end of buccal mass and curving dorsally underneath anterior esophagus. Within anterior esophagus, short, glandular midventral fold just behind odontophore. Paired ventral longitudinal folds commencing immediately behind midventral fold. Walls of anterior and midesophagus with paired, longitudinal ventral and dorsal folds; dorsal and ventral folds continuing through midesophagus and continuous with folds in posterior esophagus. Posterior esophagus with numerous folds of equal height. Midesophageal gland lacking.

Midgut. Esophagus opening to gastric chamber floor at left (Fig. 42: e). Marginal fold (Fig. 42: mf) extending anteriorly alongside major typhlosole (Fig. 42: t1), then turning posteriorly bordering edge of sorting area (Fig. 42:



FIGS. 42–44. Internal anatomy of *Limnotrochus thomsoni* (ZMB 220.065, except when noted). FIG. 42: Midgut anatomy (ZMB 220.038). Dorsal view, anterior is uppermost; FIG. 43: Circumesophageal nerve ring. Frontal view (left) and left lateral view (right); FIG. 44: Kidney anatomy. Internal view of bladder. Lateral view, anterior is at right. Roof of bladder (below intestine) cut open to reveal interior. Abbreviations: amf, accessory marginal fold; arv, afferent renal vessel; c, caecum; ce, cerebral ganglion; cf, caecal fold; cr, crescentic ridge; cu, cuticularized region in midgut roof; dd, digestive gland duct; e, esophagus; gp, glandular pad; gs, gastric shield; int, intestine; kd, kidney; mf, marginal fold; np, nephropore; pe, pedal ganglion; pl, pleural ganglion; s, septum; sa, sorting area; sb, subesophageal ganglion; sap, sorting area pad; sp, supraesophageal ganglion; ss, style sac; st, statocyst; t1, major typhlosole; u, u-shaped fold; z, zygoneury. Scale bars = 1 mm.

sa). Sorting area rectangular, with rounded posterior margin. Marginal fold elaborated into small, crescentic pad at left, posterior

tip of sorting area (Fig. 42: sap). Accessory marginal fold (Fig. 42: amf) emerging from left side of esophageal aperture, paralleling

marginal fold, curving anteriorly around posterior end of sorting area; accessory marginal fold bifurcate posteriorly. Midgut roof at left of sorting area deeply, irregularly creased, cuticularized (Fig. 42: cu). Gastric shield (Fig. 42: gs) large, continuous with cuticle of midgut roof and crystalline style pocket. Prominent fold bounding narrow depression (Fig. 42: u) below lip of style sac (Fig. 42: ss). Glandular pad (Fig. 42: gp) large, elongate, broadly rounded; accessory pad at anterior end lacking. Crescentic ridge (Fig. 42: cr) extending back from near esophageal aperture and fusing to right side of glandular pad, bounding deep, narrow crescentic groove. Proximal tip of crescentic ridge bounding deep pouch with two digestive gland ducts. Elongate, shallow caecum (Fig. 42: c) extending ventrally under glandular pad behind gastric shield. Single, elongate longitudinal fold (Fig. 42: cf) behind gastric shield, opposite caecum and glandular pad. Style sac (Fig. 34: ss) communicating proximally with intestine. Crystalline style present.

Hindgut. Proximal intestine (Fig. 34: int) passing below distal tip of style sac, then extending posteriorly alongside style sac (Fig. 34: ss), forming broad loop over proximal style sac adjacent to main gastric chamber (Fig. 34: sto). Intestine continuing forward, passing under posterior end of main kidney chamber (Fig. 34: kd), entering pallial roof between bladder (Fig. 36: b) and main kidney chamber, to papillate anus near mantle margin (Fig. 37: int). Rather voluminous periintestinal sinus surrounding pallial portion of intestine.

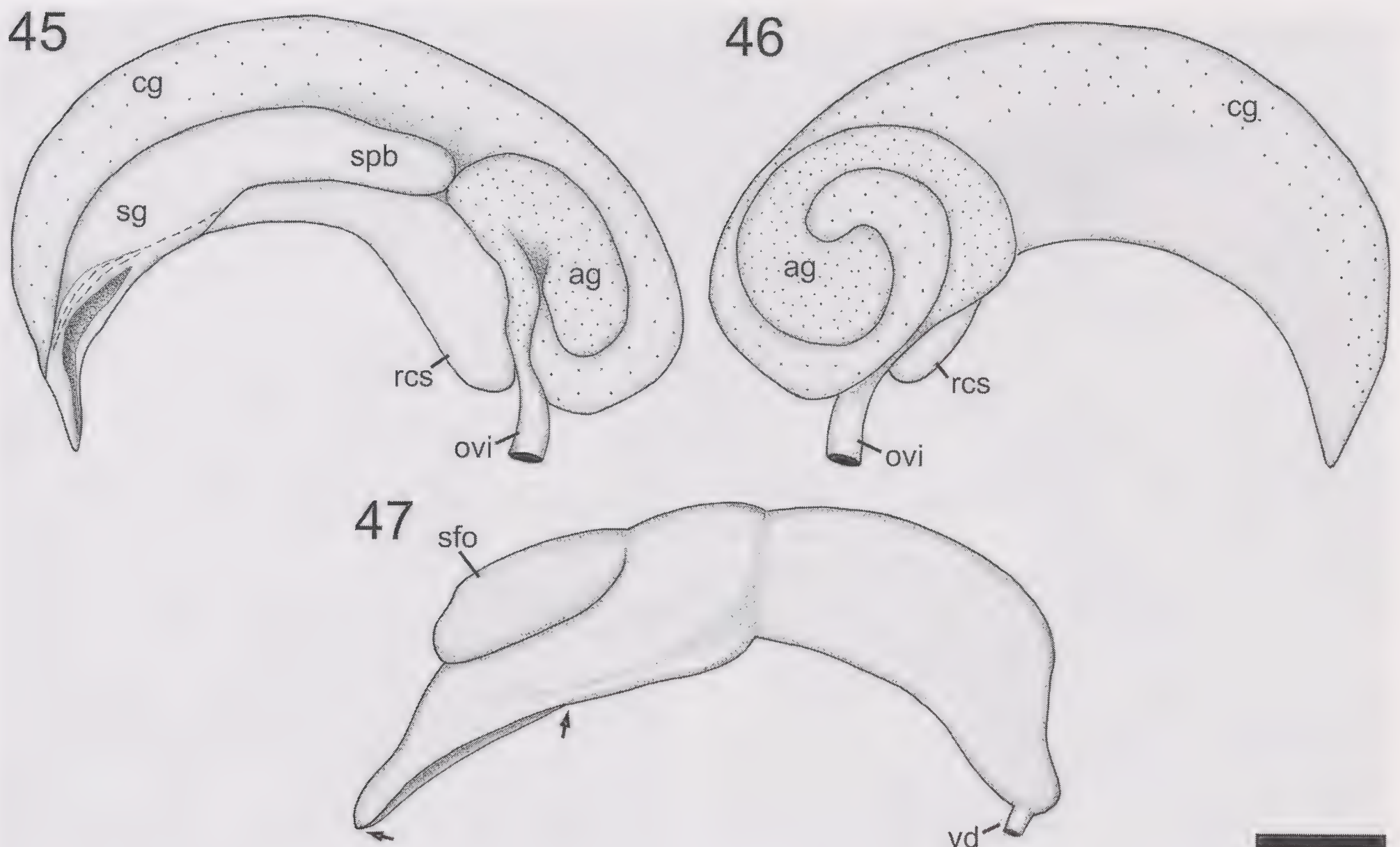
Reno-Pericardial System: Voluminous kidney (Fig. 34: kd) extending from anterior end of main gastric chamber (Fig. 34: sto) alongside style sac and pericardium into mantle roof. Kidney lumen partially subdivided into two main chambers. Main chamber (Figs. 34, 44: kd) extending full length of kidney, surrounding pericardium dorsally and at right, anteriorly overhanging base of mantle cavity; lumen mostly occluded by excretory tubules developed in roof and along walls. Large bladder (Fig. 36: b) at right of main chamber, extending into pallial roof between intestine (Fig. 36: int) and pallial gonoduct (Fig. 36: pr). Bladder (exposed chamber in Fig. 44) communicating with main chamber via small aperture (Fig. 44: arrow) just behind afferent renal vessel (Fig. 44: arv). Bladder

partially subdivided posteriorly by incomplete horizontal septum of excretory tissue (Fig. 44: s), separating elongate chamber below. Large sheet of excretory tubules branching from afferent renal vessel and extending anteriorly along bladder floor, partially separating shallow ventral chamber below. Nephridial gland absent.

Narrow, deep pericardium (Fig. 34: per) extending underneath kidney alongside style sac (Fig. 34: ss) to intestinal loop.

Nervous System: Cerebral ganglia (Fig. 43: ce) separated by slight constriction, each ganglion producing six nerves (optic, statocyst, tentacular, and three labial nerves). Buccal ganglia lying ventrolaterally at base of buccal mass, at inner edge of retractor muscles, below anterior esophagus. Pleural ganglia (Fig. 43: pl) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives; left connective producing two small nerves. Pedal ganglia (Fig. 43: pe) with two prominent anterior nerves and approximately six smaller accessory nerves. Statocysts (Fig. 43: st) with numerous angular statoconia present dorsally alongside pedal ganglia behind pedal connectives. Subesophageal ganglion (Fig. 43: sb) joined to left pleural ganglion by short, thick connective; connective producing one stout nerve. In addition to connectives to left pleural and visceral ganglia, subesophageal ganglion producing one stout, branching nerve, two fine accessory nerves and zygoneurous connection to right pleural ganglion (Fig. 43: z). Long connective uniting right pleural and supraesophageal ganglia (Fig. 43: sp), the latter lying at left of midesophagus (see Fig. 37: sp). Dialyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supraesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present at base of cephalic hemo-coel (Fig. 37: vg).

Female Reproductive System: Gonad (Fig. 36: te) dorsally overlying digestive gland (Fig. 36: dg) from tip of visceral mass to posterior end of gastric chamber (Fig. 36: sto). Oviduct emerging ventrally from ovary. Renal oviduct (Figs. 45, 46: ovi) entering glandular oviduct at base of mantle cavity. Pallial oviduct, with proximal albumen (Figs. 45, 46: ag) and distal capsule glands (Figs. 45, 46: cg). Albumen gland forming rear-facing c-shaped tube

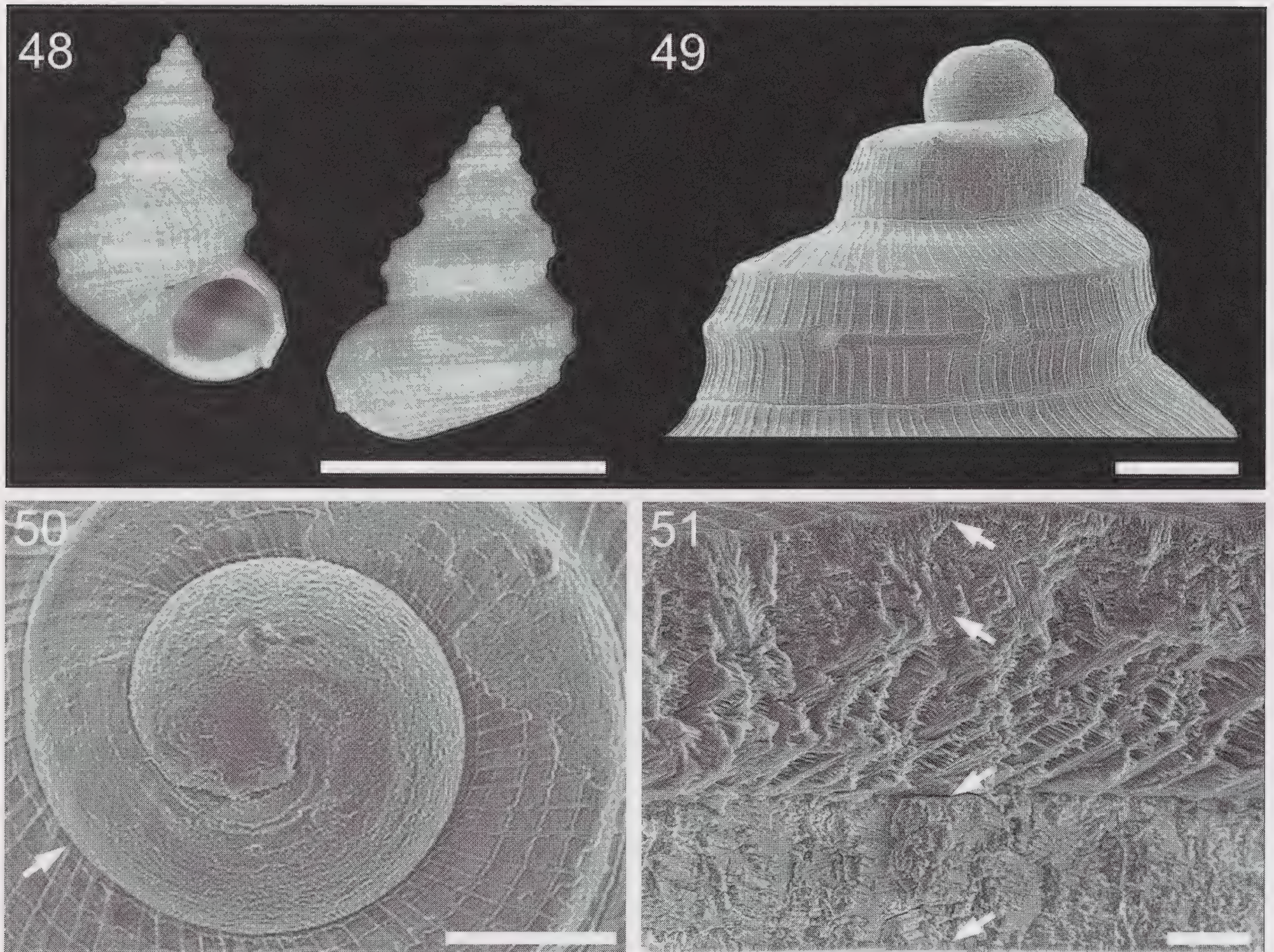


FIGS. 45–47. Reproductive anatomy of *Limnotrochus thomsoni* (ZMB 220.038, except when noted). FIG. 45: External, left lateral view of pallial oviduct. Anterior is at left. Double dashed line indicates opening from bursa to gonoductal groove; single dashed line indicates continuation of inner edge of medial lamina as shallow groove to opening of seminal receptacle; FIG. 46: External, right lateral view of pallial oviduct. Anterior is at right; FIG. 47: External, left lateral view of prostate (ZMB 220.065). Anterior is at left. Arrows indicate extent of opening to gonoductal groove. Prominent grooves of lateral lamina seen by transparency. Abbreviations: ag, albumen gland; cg, capsule gland; ovi, renal oviduct; rcs, seminal receptacle; sfo, spermatophore forming organ; sg, seminal groove; spb, spermatophore bursa; vd, vas deferens. Scale bar = 1 mm.

at posterior end of pallial oviduct; capsule gland developed along dorsal crest of pallial oviduct. Glandular tissue of capsule and albumen glands with opposing flattened surfaces bounding morphologically dorsal gonoductal groove. Narrow vagina along anterior one fourth of oviduct opening to sperm gutter (Fig. 45: sg) in median lamina. Gutter leading posteriorly to elongate, narrow spermatophore bursa (Fig. 45: spb). Inner wall of median lamina fusing to outer wall, restricting communication between spermatophore bursa and gonoductal groove to short, anterior slit (Fig. 45: double dashed line). Ventral edge of median lamina inner wall (Fig. 45: single dashed line) continuing posteriorly as shallow groove above ventral channel, posteriorly enclosing entrance to seminal receptacle (Figs. 45, 46: rcs). Communication between sperm gutter and ventral channel bounded by shallow fold extending along ventral edge of vagina.

Male Reproductive System: Narrow vas deferens (Fig. 47: vd) emerging ventrally from testes (Figs. 34, 36: te), entering posterior end of prostate at base of mantle cavity. Short distal portion of vas deferens thickened and forming straight seminal vesicle. Prostate glandular, forming flattened tube, opening to mantle cavity through narrow, ventral slit along anterior one third (arrows). Posterior half of prostate separated from anterior half by slight dorsal constriction. Glands of posterior lateral lamina deeply longitudinally grooved. Posterior medial lamina more weakly and irregularly longitudinally grooved. Dorsal, anterior portion of prostate forming short, thick, glandular, tube-like spermatophore-forming organ (Fig. 47: sfo). Organ terminating blindly anteriorly, communicating posteriorly with gonoductal groove via narrow aperture.

Remarks: The anatomy was also described by Digby (1902) who, as for *Chytra*, provided a



FIGS. 48–51. Shell morphology of *Mysorelloides multisulcata* (IRSNB no. 126). FIG. 48: Adult shell of specimen used in anatomical investigations. Scale bar = 5 mm; FIG. 49: Embryonic shell. Scale bar = 200 μ m; FIG. 50: Embryonic shell, apical view. Arrow indicates approximate transition to teleoconch. Scale bar = 100 μ m; FIG. 51: Shell microstructure. Cross section through shell parallel to aperture; outside of shell is uppermost. Order of layers from external to internal: (a) irregular, simple prismatic structure, (b) simple radial crossed lamellar structure, (c) simple comarginal crossed lamellar structure, (d) irregular, complex crossed lamellar structure, (e) irregular, simple prismatic structure. Arrows indicate transitions between layers. Scale bar = 20 μ m.

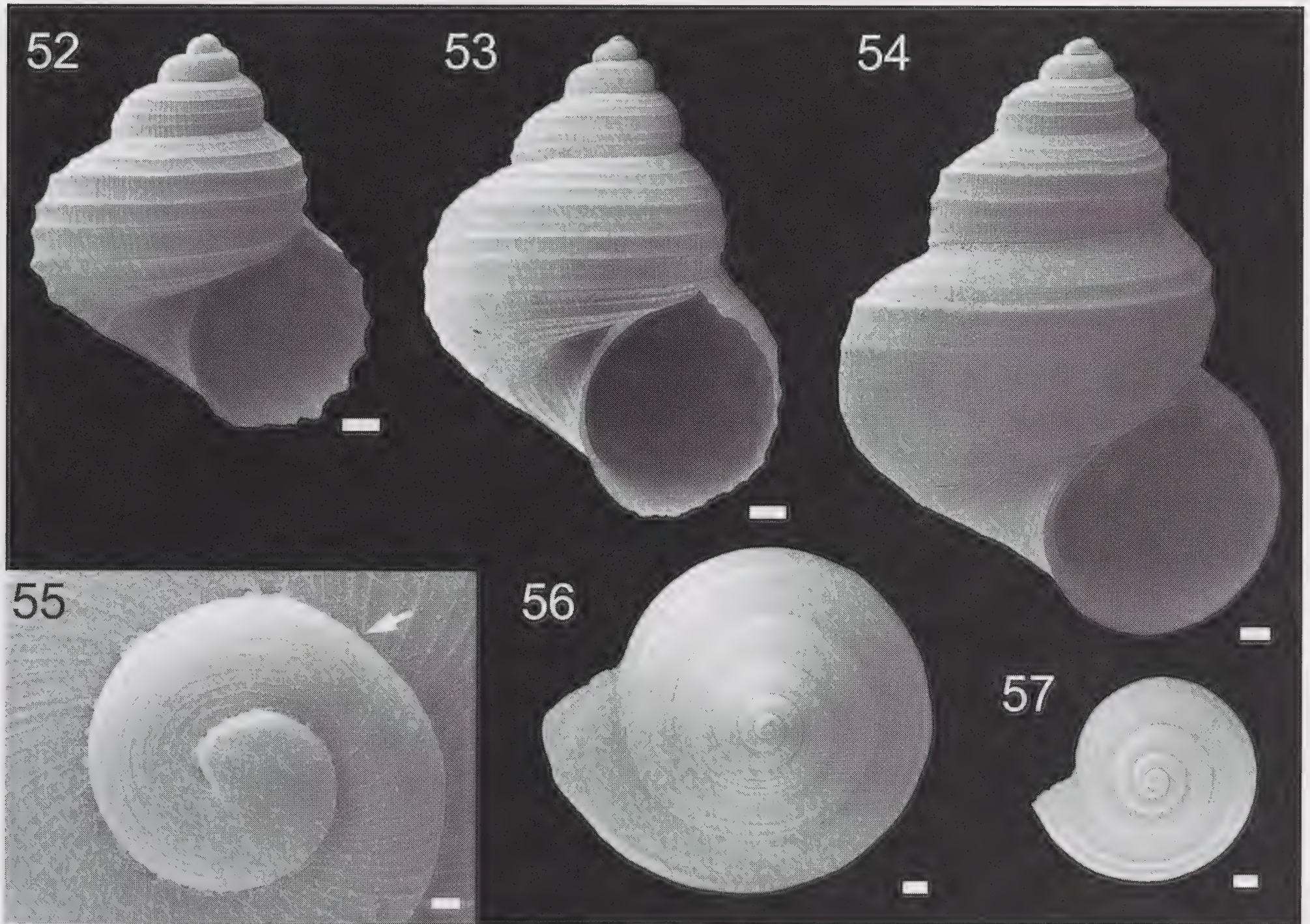
rather accurate but not very detailed description of most features. Although Digby (1902) found the anatomy of *Limnotrochus* and *Chytra* to be distinctly similar, she remarked that the affinities of the former were even more difficult to assess. She concluded *Limnotrochus* to be allied to *Chytra* and *Tiphobia*, but likely more near the “stromboid” group (i.e., *Strombus*, *Aporrhais*). Moore (1903) reproduced parts of Digby’s (1902) description, and featured an operculum, one row of the radula and the interior of the midgut.

Brown (1994) remarked on the variability in size and number of denticles on radular teeth in comparing the specimen figured by Digby (1902) to one he examined from Kombe, Zambia. West & Cohen (1996) reported three layers of crossed lamellar microstructure in the shell.

Mysorelloides multisulcata
(Bourguignat, 1888)

Material Examined: Democratic Republic of Congo: Kalemie (DBL) (4 spms). Tanzania: at Karema, in intestine of the fish *Synodontis melanostictus*, ± 30 m (IRSNB no. 123) (4 spms); at Karema (IRSNB no. 126) (8 spms; 2 spms dissected). Zambia: between Butondwe and Kumbula Island, 50 m (DBL) (47 spms).

Shell: Adult shell comprising up to five whorls (Figs. 48, 54). Apical cap of embryonic shell with irregularly, finely textured surface, rapidly giving way to numerous fine spiral threads (Figs. 49, 50, 55). Gradual transition to teleoconch with spiral threads joined by fine axial threads and variable number of prominent,



FIGS. 52–57. Shell morphology of *Mysorelloides multisulcata* (DBL). FIG. 52: Juvenile shell. Scale bar = 200 μ m; FIG. 53: Juvenile shell. Scale bar = 300 μ m; FIG. 54: Shell of sub-adult. Scale bar = 200 μ m; FIG. 55: Embryonic shell, apical view. Arrow indicates approximate transition to teleoconch. Scale bar = 20 μ m; FIG. 56: Sub-adult, apical view (same specimen as in FIG. 54). Scale bar = 200 μ m; FIG. 57: Juvenile, apical view (same specimen as in FIG. 52). Scale bar = 200 μ m.

smoothly undulating spiral cords producing reticulate pattern. Spiral threads gradually becoming obsolete over first three teleoconch whorls. Several spiral cords may be more prominent, producing angular whorl profile (Fig. 48), or spiral cords may be more or less equal in prominence and distributed over smoothly rounded whorls (Figs. 52–54). Aperture thickened, holostome. Umbilicus narrow. Shell microstructure (Fig. 51) comprising five layers from external to internal: (1) irregular, simple prismatic structure, (2) simple radial crossed lamellar structure, (3) simple comarginal crossed lamellar structure, (4) irregular, complex crossed lamellar structure, (5) irregular, simple prismatic structure.

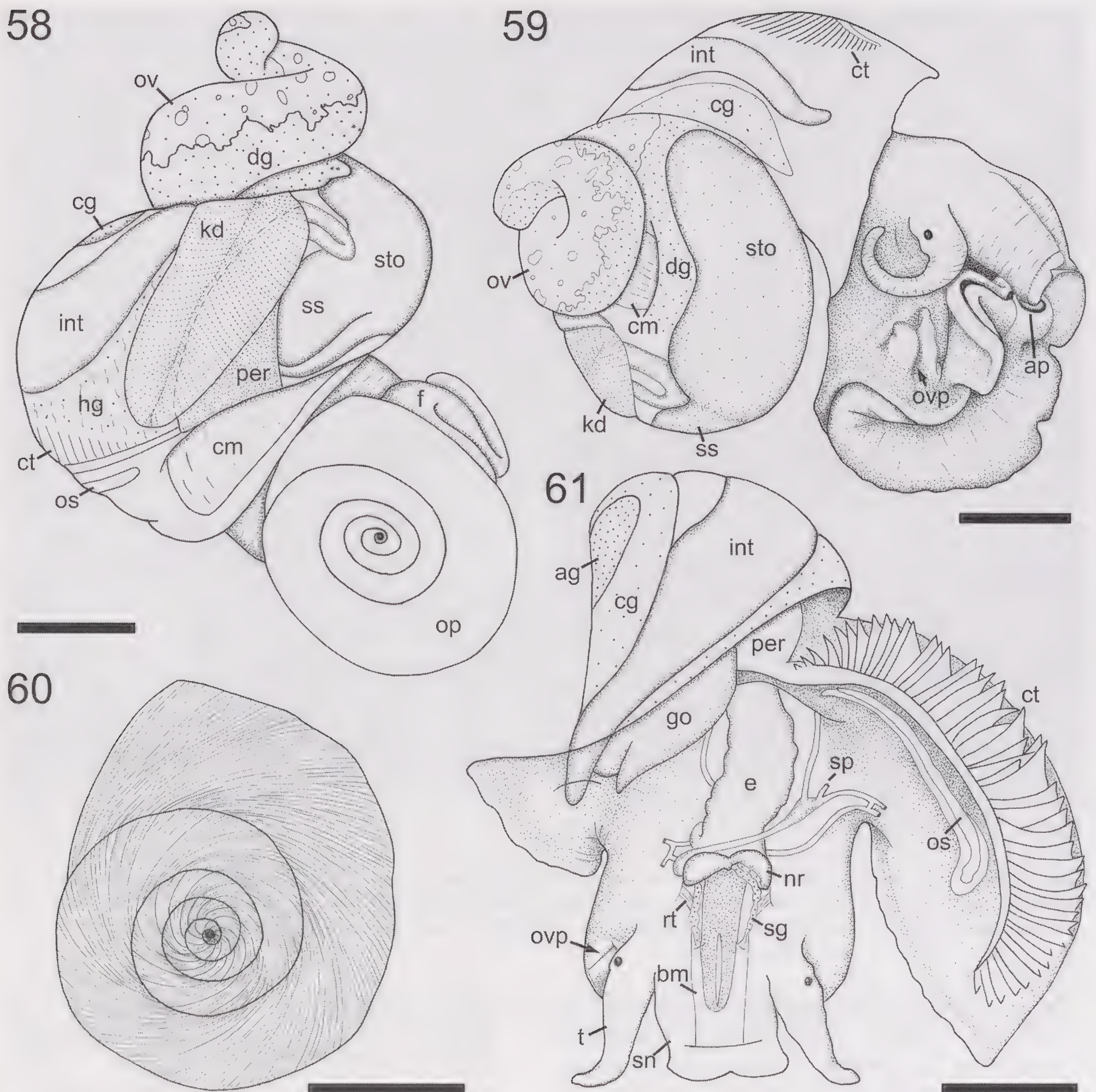
External Anatomy: Operculum (Fig. 60) thin, transparent, light amber brown in color. Operculum spiral, comprising approximately 5 whorls, increasing evenly in size.

Foot narrowly ovate, with broad propodium bearing shallow pedal gland along anterior

margin (Fig. 59: ap). Columellar muscle extending to base of mantle cavity. In females, ovipositor (Fig. 59: ovp) present on right side of foot, below eye, just behind foot sole margin at junction between propodium and mesopodium. Aperture of ovipositor forming simple, oblique slit bounded by tall folds; lumen shallow, u-shaped with prominent fold projecting from floor. Finely grooved tract to foot sole and ciliated egg groove between ovipositor and pallial oviduct lacking.

Retracted cephalic tentacles (Fig. 61: t) rather smooth, long, tapering, slightly longer than snout. Eyes located on small protuberances at base of tentacles. Snout (Fig. 61: sn) broad, squarish, with small mouth opening ventrally at tip.

Mantle cavity short, extending approximately one half whorl. Hypobranchial gland weakly developed (Fig. 58: hg). Mantle edge smooth. Ctenidium (Figs. 58, 59, 61: ct) extending from near mantle margin to rear of mantle cavity; leaflets narrowly triangular.

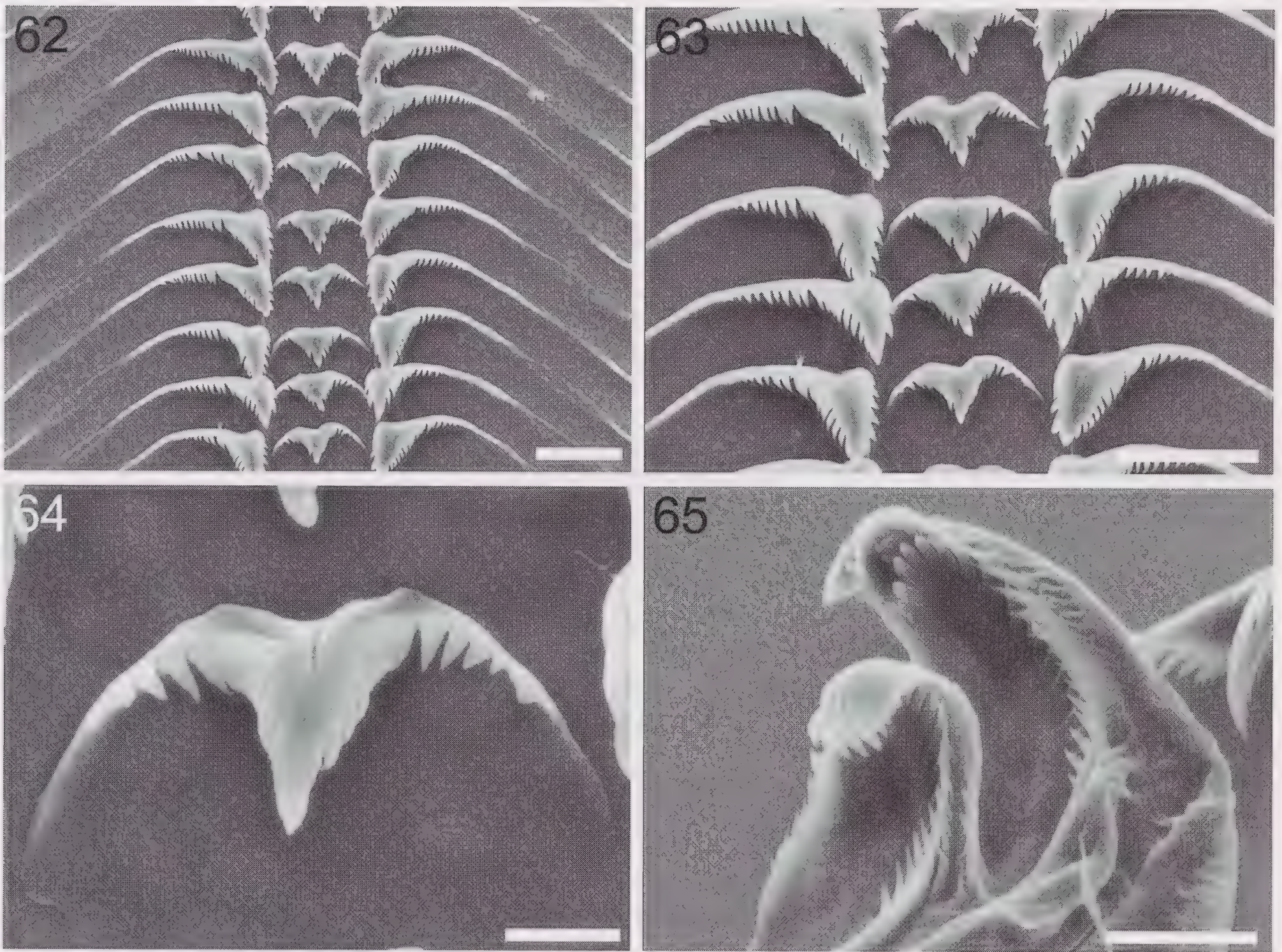


FIGS. 58–61. External anatomy of *Mysorelloides multisulcata* (IRSNB no. 126). FIG. 58: External view of organs in visceral mass. Dashed line indicates extent of pericardium under main kidney chamber; FIG. 59: External view of organs in visceral mass; right lateral view of female head-foot with ovipositor; FIG. 60: Operculum; FIG. 61: Dorsal view of mantle cavity and organs of cephalic hemocoel seen by transparency. Anterior is below. Abbreviations: ag, albumen gland; ap, anterior pedal gland; bm, buccal mass; cg, capsule gland; cm, columellar muscle; ct, ctenidium; dg, digestive gland; e, esophagus; go, pallial gonoduct; hg, hypobranchial gland; int, intestine; kd, kidney; nr, circumesophageal nerve ring; op, operculum; os, osphradium; ov, ovary; ovp, ovipositor; per, pericardium; rt, buccal retractor; sg, salivary gland; sn, snout; sp, supraesophageal ganglion; ss, style sac; sto, stomach; t cephalic tentacle. Scale bars = 1 mm.

Osphradium (Figs. 58, 61: os) smooth, long, roughly two thirds of ctenidium in length, in shallow depression.

Alimentary System: Foregut. Radula taenioglossate (Fig. 62). Rachidian (Fig. 63) rectangular, wider than tall, with lower margin

tapering to narrow, squarish projection. Upper margin convex to slightly concave, with cutting edge bearing single, prominent, pointed central cusp bounded by six to 14 fine, pointed denticles on each side (Fig. 64); denticles often fused to each other and to central cusp. Lateral teeth with very long

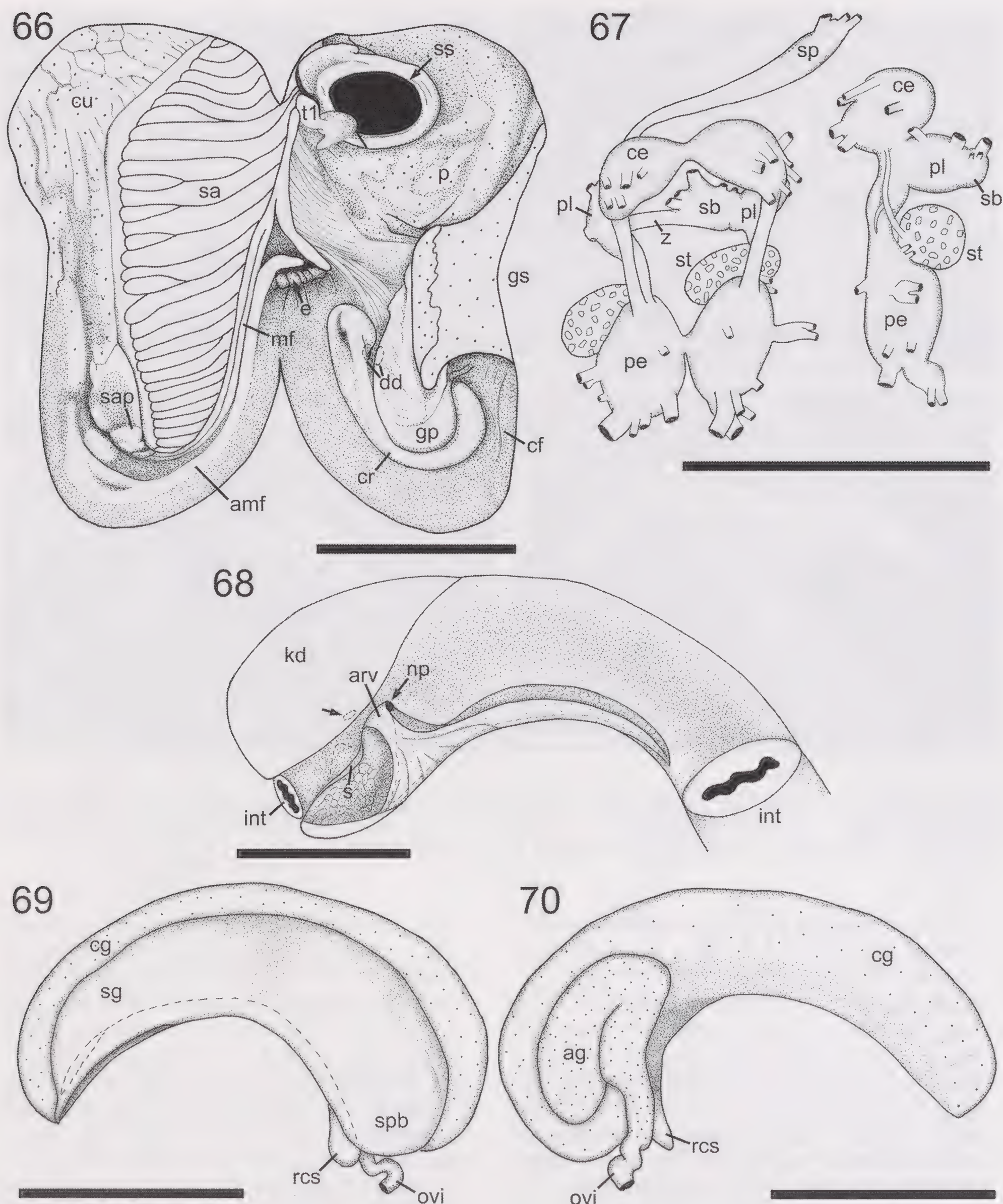


FIGS. 62-65. Radula morphology of *Mysorelloides multisulcata* (IRSNB no. 126). FIG. 62: Rachidian and lateral teeth. Scale bar = 20 μ m; FIG. 63: Rachidian and lateral teeth. Scale bar = 20 μ m; FIG. 64: Rachidian. Scale bar = 5 μ m; FIG. 65: Marginal teeth. Scale bar = 10 μ m.

lateral extensions (Fig. 62), roughly twice as long as cutting edge. Cutting edge triangular with five to seven inner and 17–23 outer pointed denticles. Marginal teeth (Fig. 65) long, slender, with narrow, elongate, rounded tips bearing numerous fine, pointed denticles; inner marginal with ~20–25 denticles around tip and along inner edge only, outer marginal with ~30–35 denticles along distal one third of inner and outer edges. Number of denticles on all teeth variable between individuals.

Mouth opening ventrally at anterior end of snout. Buccal mass (Fig. 61: bm) narrow, elongate; small odontophore occupying posterior half of buccal cavity. Narrowly triangular, glandular subradular organ extending along floor of buccal cavity at anterior end of odontophore. Small, paired jaw dorsally flanking mouth at anterior ends of dorsal folds. Shallow, nonglandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear of buccal cavity. Salivary glands (Fig. 61: sg) forming

short, coiled, unbranched tubules, opening dorsolaterally alongside odontophore. Salivary glands asymmetrical with left gland overlying circumesophageal nerve ring (Fig. 61: nr), and right gland terminating within nerve ring. Thick buccal retractors (Fig. 61: rt) extending from rear wall of buccal mass, inserting on lateral walls of cephalic hemocoel immediately anterior to nerve ring. Nerve ring lying short distance back from posterior end of cephalic tentacles. Radular sac short, projecting slightly past end of buccal mass and curving dorsally underneath anterior esophagus. Within anterior esophagus, short, glandular midventral fold just behind odontophore. Paired ventral longitudinal folds commencing immediately behind midventral fold. Walls of anterior and midesophagus with paired, longitudinal ventral and dorsal folds and numerous additional, longitudinal folds of roughly equal prominence; dorsal and ventral folds fusing with each other (i.e., right dorsal fold with right ventral fold) at posterior



FIGS. 66–70. Internal anatomy of *Mysorelloides multisulcata* (IRSNB no. 126). FIG. 66: Midgut anatomy. Dorsal view, anterior is uppermost; FIG. 67: Circumesophageal nerve ring. Frontal view (left) and left lateral view (right); FIG. 68: Kidney anatomy. Internal view of bladder. Lateral view, anterior is at right. Roof of bladder (below intestine) cut open to reveal interior; FIG. 69: External, left lateral view of pallial oviduct. Anterior is at left; FIG. 70: External, right lateral view of pallial oviduct. Anterior is at right. Abbreviations: ag, albumen gland; amf, accessory marginal fold; arv, afferent renal vessel; ce, cerebral ganglion; cf, caecal fold; cg, capsule gland; cr, crescentic ridge; cu, cuticularized region in midgut roof; dd, digestive gland duct; e, esophagus; gp, glandular pad; gs, gastric shield; int, intestine; kd, kidney; mf, marginal fold; np, nephropore; ovi, renal oviduct; p, crystalline style pocket; pe, pedal ganglion; pl, pleural ganglion; rcs, seminal receptacle; sa, sorting area; sb, subesophageal ganglion; sap, sorting area pad; sg, seminal groove; sp, supraesophageal ganglion; spb, spermatophore bursa; ss, style sac; st, statocyst; t1, major typhlosole; z, zygoneury. Scale bars = 1 mm.

end of midesophagus, enclosing shallow, smooth, rear-projecting triangular troughs. Midesophageal gland lacking.

Midgut. Esophagus opening to gastric chamber floor at left (Fig. 66: e). Marginal fold (Fig. 66: mf) extending anteriorly alongside major typhlosole (Fig. 66: t1), then turning posteriorly bordering edge of sorting area (Fig. 66: sa). Sorting area rectangular, with rounded posterior margin. Marginal fold elaborated into small pad at left, posterior tip of sorting area (Fig. 66: sap). Accessory marginal fold (Fig. 66: amf) emerging from left side of esophageal aperture, paralleling marginal fold, curving anteriorly around posterior end of sorting area; accessory marginal fold bifurcate posteriorly. Epithelium of midgut floor finely, regularly grooved at right of marginal fold and along projecting tip of major typhlosole. Anterior midgut roof at left of sorting area deeply, irregularly creased, cuticularized (Fig. 66: cu). Gastric shield (Fig. 66: gs) moderately large, continuous with cuticle of midgut roof and crystalline style pocket (Fig. 66: p). Creased, weakly developed fold bounding grooved u-shaped depression below lip of style sac (Fig. 66: ss) in one of two specimens examined. Glandular pad (Fig. 66: gp) small, broadly rounded; accessory pad at anterior end lacking. Crescentic ridge (Fig. 66: cr) extending back from near esophageal aperture and fusing to right side of glandular pad, bounding deep, narrow crescentic groove. Proximal tip of crescentic ridge bounding deep pouch with two digestive gland ducts. Caecum lacking. Single, weakly developed longitudinal fold (Fig. 66: cf) behind gastric shield, opposite glandular pad. Style sac (Fig. 58: ss) communicating proximally with intestine. Crystalline style present.

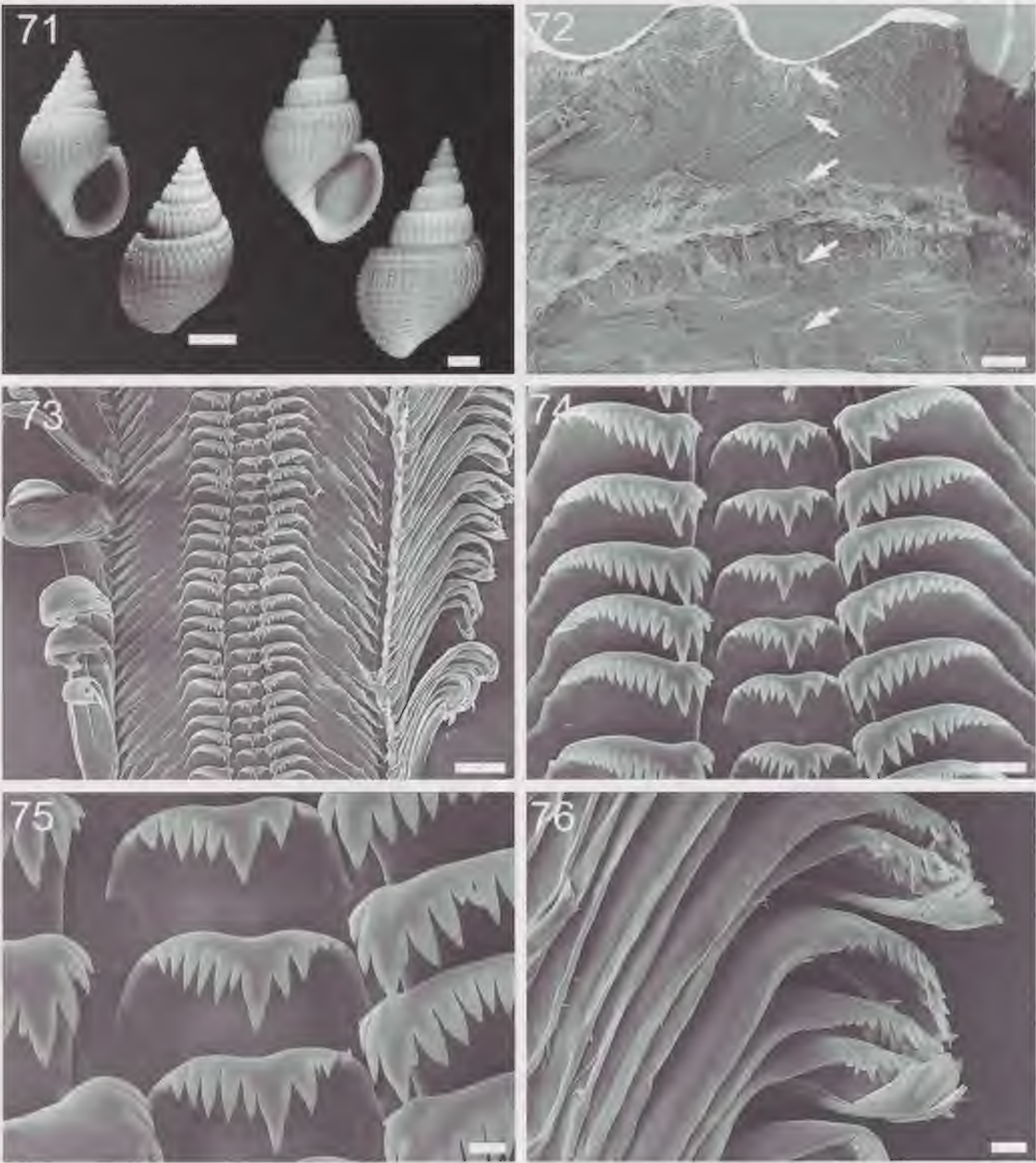
Hindgut. Proximal intestine (Fig. 58: int) passing below distal tip of style sac, then extending posteriorly alongside style sac (Fig. 58: ss), forming small loop across right side proximal style sac adjacent to main gastric chamber (Fig. 58: sto). Intestine continuing forward, passing under posterior end of main kidney chamber (Fig. 58: kd), entering pallial roof between bladder and main kidney chamber, to papillate anus near mantle margin (Fig. 61: int).

Reno-Pericardial System: Voluminous kidney (Fig. 58: kd) extending from near anterior end of main gastric chamber (Fig. 58: sto) alongside style sac and pericardium into mantle

roof. Kidney lumen partially subdivided into two main chambers. Main chamber (Figs. 58, 68: kd) extending full length of kidney, surrounding pericardium dorsally and at right, anteriorly overhanging base of mantle cavity; lumen mostly occluded by excretory tubules developed in roof and along walls. Small bladder at right of main chamber, extending into pallial roof between intestine (Fig. 58: int) and pallial gonoduct (Fig. 58: cg). Bladder (exposed chamber in Fig. 68) communicating with main chamber via small aperture (Fig. 68: arrow) just behind afferent renal vessel (Fig. 68: arv). Bladder partially subdivided posteriorly by incomplete horizontal septum of excretory tissue (Fig. 68: s), separating shallow, narrow chamber above. Large sheet of excretory tubules branching from afferent renal vessel and extending anteriorly along bladder floor, partially separating narrow, shallow ventral chamber below. Nephridial gland absent.

Narrow, deep pericardium (Fig. 58: per) extending underneath kidney alongside style sac (Fig. 58: ss) past intestinal loop.

Nervous System: Cerebral ganglia (Fig. 67: ce) connected by short, stout commissure, each ganglion producing six nerves (optic, statocyst, tentacular, and three labial nerves). Buccal ganglia lying ventrolaterally at base of buccal mass, at inner edge of retractor muscles, below anterior esophagus. Pleural ganglia (Fig. 67: pl) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives. Pedal ganglia (Fig. 67: pe) with two prominent anterior nerves and approximately five to seven smaller accessory nerves. Statocysts (Fig. 67: st) with numerous angular statoconia present dorsally alongside pedal ganglia behind pedal connectives. Subesophageal ganglion (Fig. 67: sb) separated from left pleural ganglion by slight constriction. In addition to connectives to left pleural and visceral ganglia, subesophageal ganglion producing two stout nerves, two fine nerves and zygoneurous connection to right pleural ganglion (Fig. 67: z). Long connective uniting right pleural and supraesophageal ganglia (Fig. 67: sp), the latter lying at left of midesophagus (see Fig. 61: sp). Dialyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supraesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present at base of cephalic hemocoel.



FIGS. 71–76. Shell and radula morphology of *Paramelania iridescens* (ZMB 220.037, except when noted). FIG. 71: Adult shell. At left, shell of specimen used in anatomical investigations; at right, more mature specimen (USNM 857897). Scale bar = 5 mm; FIG. 72: Shell microstructure. Cross section through shell parallel to aperture; outside of shell is uppermost. Order of layers from external to internal: (a) irregular, simple prismatic structure, (b) simple radial crossed lamellar structure, (c) simple comarginal crossed lamellar structure, (d) simple radial crossed lamellar structure, (e) irregular, complex crossed lamellar structure, (f) irregular, simple prismatic structure. Arrows indicate transitions between layers. Scale bar = 100 µm; FIG. 73: Radula. Scale bar = 40 µm; FIG. 74: Rachidian and lateral teeth. Scale bar = 10 µm; FIG. 75: Rachidian. Scale bar = 2 µm; FIG. 76: Marginal teeth. Scale bar = 6 µm.

Female Reproductive System: Gonad (Figs. 58, 59: ov) dorsally overlying digestive gland (Fig. 59: dg) from tip of visceral mass to

posterior end of gastric chamber (Fig. 59: sto). Oviduct emerging ventrally from ovary. Renal oviduct (Figs. 69, 70: ovi) forming short

recurvent loop behind mantle cavity before entering base of glandular oviduct. Pallial oviduct, with proximal albumen (Fig. 70: ag) and distal capsule glands (Figs. 69, 70: cg). Albumen gland forming rear-facing c-shaped tube at posterior end of pallial oviduct; capsule gland developed along dorsal crest of pallial oviduct. Glandular tissue of capsule and albumen glands with opposing flattened surfaces bounding morphologically dorsal gonoductal groove. Narrow vagina along anterior one third of oviduct opening to sperm gutter (Fig. 69: sg) in median lamina. Gutter leading posteriorly to elongate, broad spermatophore bursa (Fig. 69: spb). Inner wall of median lamina fusing to outer wall, restricting communication between spermatophore bursa and ventral channel to short, anterior slit (Fig. 69: double dashed line). Ventral edge of median lamina inner wall (Fig. 69: single dashed line) continuing posteriorly as shallow groove above ventral channel, posteriorly enclosing entrance to seminal receptacle (Figs. 69, 70: rcs). Communication between sperm gutter and ventral channel bounded by two folds: one shallow dorsal fold along outer ventral edge of median lamina inner wall, and one prominent ventral fold extending along ventral edge of vagina. Dorsal and ventral fold fusing posteriorly, continuing as single, prominent longitudinal fold along length of bursa floor with central longitudinal gutter continuous with communication to ventral channel.

Male Reproductive System: Male reproductive anatomy unknown.

Remarks: Leloup (1953) reported the operculum to be spiral, a rachidian broader than tall with 9–11/1/9–11; lateral teeth with 3–4/1/~20; marginal teeth with ~20/~15. Riedel (1993) provided a description of the embryonic shell, including SEM micrographs, of *M. multisulcata* specimens misidentified as *Limnotrochus thomsoni* (fig. 21; pl. 4, figs. 5, 6).

Paramelania iridescens
(Moore, 1898)

Material Examined: (DBL) (1 spm); (USNM 250717) (1 spm); (ZMB 52.540) (1 spm); (ZMB 53.548) (1 spm); (ZMB 55.030) (1 spm); (ZMB 85.792) (1 spm); (ZMB 92.364) (2 spms); (CM 62.29277) (3 spms); (CM 62.29435) (3 spms); (NHMB 10.846a) (1 spm). Burundi: Nyanza-Lac, 2 km SW Military Point, 20 m (04°21'S, 29°36'E) (USNM 882019) (5

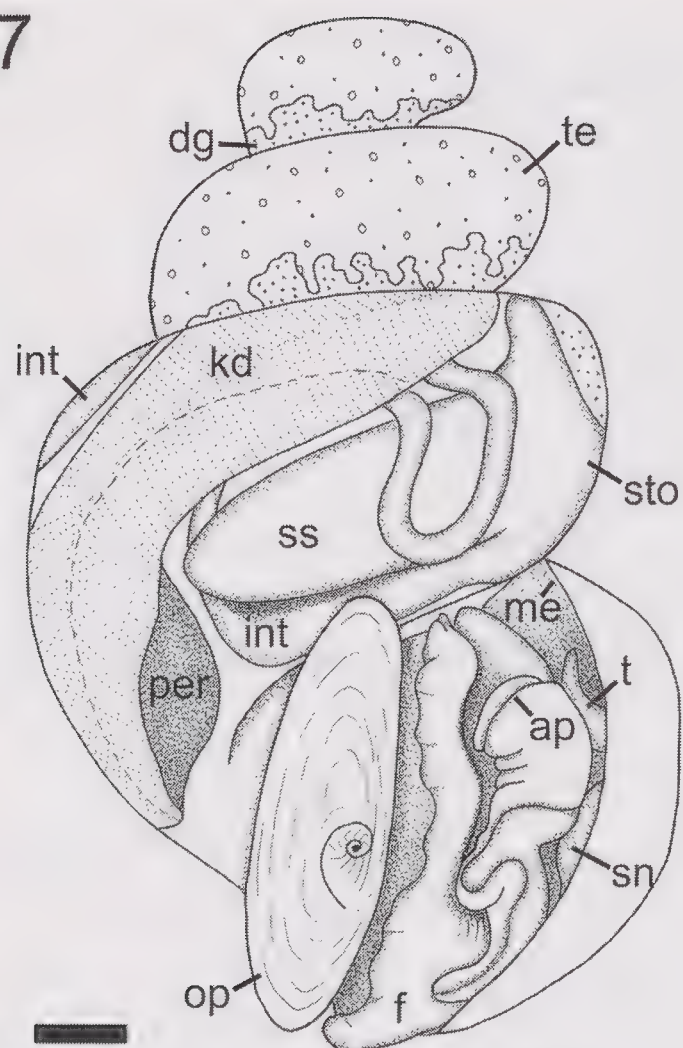
spms); Bujumbura (ZMB 220.053) (2 spms); same (ZMB 220.163) (3 spms); same (ZMB 220.164) (2 spms). Tanzania: Kigoma (ZMB 85.792) (1 spm); same (ZMB 220.120) (29 spms); same (ZMB 220.037) (4 spms; 3 spms dissected); between Kigoma & Ujiji, 35–60 m (ZMB 220.173) (2 spms); Viapili, 100–120 ft (07°27'S, 30°37'E) (USNM 857897) (2 spms). Zambia: Chipata Bay, 80 m (08°41.700'S, 31°08.952'E) (ZMB 220.099) (1 spm dissected); Mpulungu, 30 m (DBL) (5 spms).

Shell: Adult shell comprising up to nine whorls, typically with broken apex (Fig. 71). Embryonic shell unknown. Early teleoconch whorls rapidly developing roughly five to six spiral threads and closely packed fine axial threads producing reticulate appearance. By third teleoconch whorl, opisthocyrt axial ribs appearing, producing nodes at intersection with axial threads. Nodes on uppermost spiral thread gradually becoming more prominent, and thread may be slightly separated from remaining, regularly spaced threads. Uppermost thread also slightly separated from suture, producing flattened shoulder. Number of spiral threads above suture rather constant through ontogeny. Whorl profile on early teleoconch whorls may be rounded or more angular in specimens with early development of flattened shoulder; later whorls gradually becoming more flattened. Aperture thickened, slightly flaring, with weakly developed anterior and posterior siphon. Single spine may be developed on shoulder above posterior siphon in adults. Umbilicus lacking. Shell microstructure (Fig. 72) comprising six layers from external to internal: (1) irregular, simple prismatic structure, (2) simple radial crossed lamellar structure, (3) simple comarginal crossed lamellar structure, (4) simple radial crossed lamellar structure, (5) irregular, complex crossed lamellar structure, (6) irregular, simple prismatic structure.

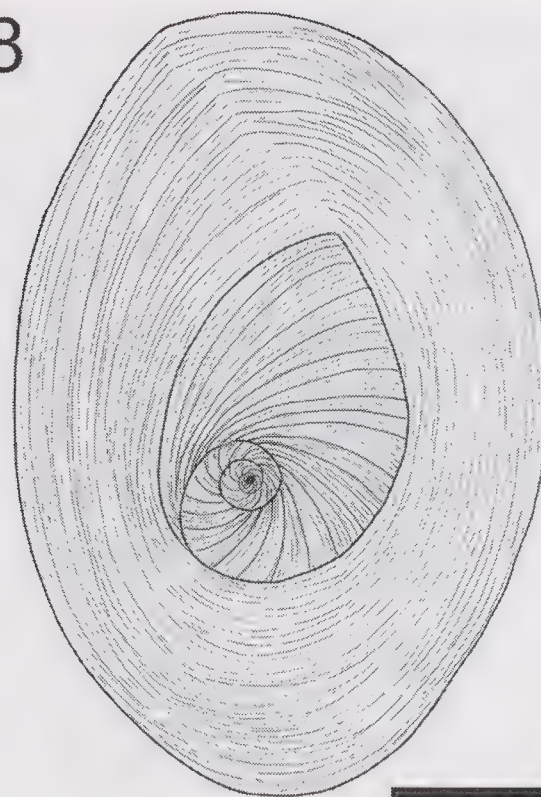
External Anatomy: Operculum (Fig. 78) thick, concave, dark brown in color. Operculum concentric with central, paucispiral nucleus; nucleus comprising approximately three whorls.

Foot broadly ovate, with broad propodium bearing shallow pedal gland (Fig. 77: ap) along anterior margin. In females, ovipositor present on right side of foot, below eye, just behind foot sole margin. Aperture of ovipositor forming simple, oblique slit on slight rise. Finely grooved tract to foot sole and ciliated

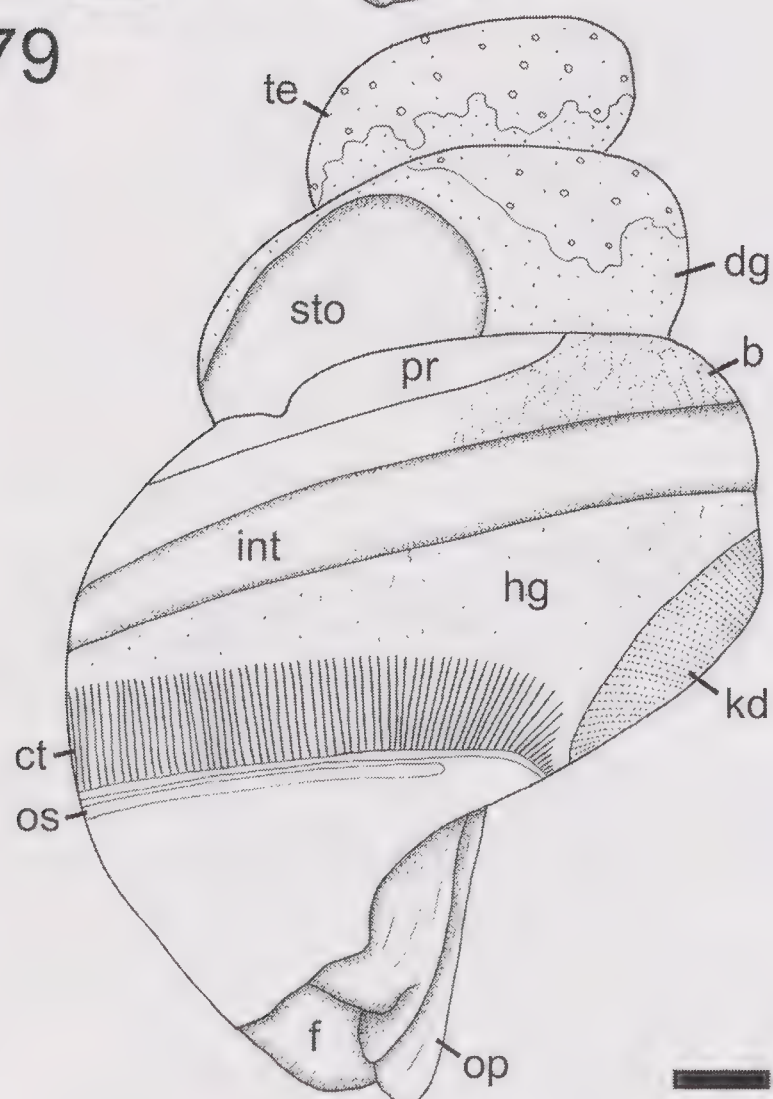
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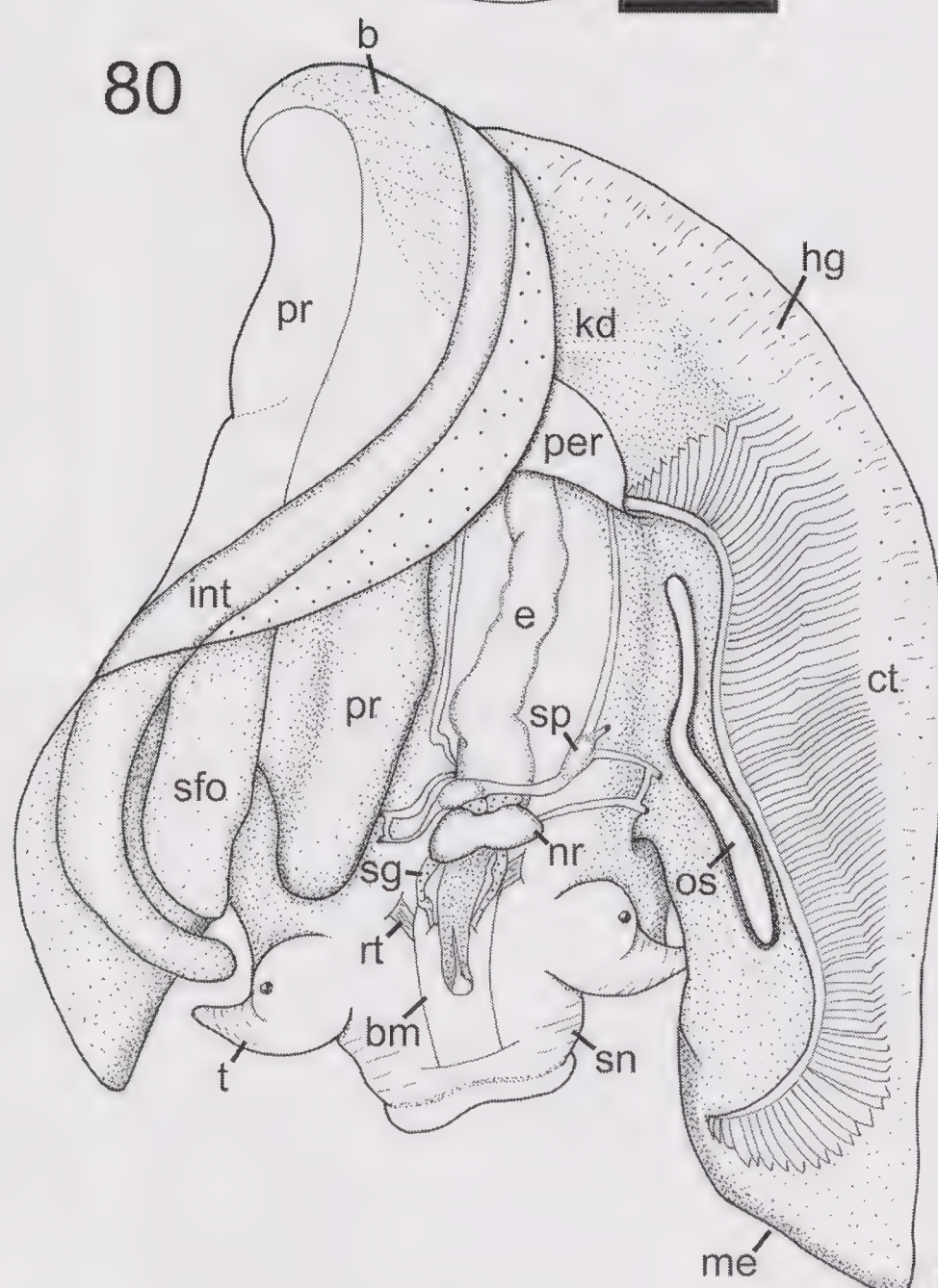
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FIGS. 77–80. External anatomy of *Paramelania iridescens* (ZMB 220.037). FIG. 77: External view of organs in visceral mass. Dashed line indicates extent of pericardium under main kidney chamber; FIG. 78: Operculum; FIG. 79: External view of organs in visceral mass; FIG. 80: Dorsal view of mantle cavity and organs of cephalic hemocoel seen by transparency. Anterior is below. Abbreviations: ap, anterior pedal gland; b, bladder; bm, buccal mass; cm, columellar muscle; ct, ctenidium; dg, digestive gland; e, esophagus; f, foot; hg, hypobranchial gland; int, intestine; kd, kidney; me, mantle edge; nr, circumesophageal nerve ring; op, operculum; os, osphradium; per, pericardium; pr, prostate; rt, buccal retractor; sfo, spermatophore forming organ; sg, salivary gland; sn, snout; sp, supraesophageal ganglion; ss, style sac; sto, stomach; t, cephalic tentacle; te, testis. Scale bars = 1 mm.

egg groove between ovipositor and pallial oviduct lacking.

Retracted cephalic tentacles (Figs. 77, 80: t) smooth, short, triangular, slightly shorter

than snout in length. Eyes located on small protuberances at base of tentacles. Snout (Figs. 77, 80: sn) broad, squarish, with small mouth opening ventrally at tip.

Mantle cavity short, extending approximately one half whorl. Hypobranchial gland moderately well developed (Figs. 79, 80: hg), with transverse grooves. Mantle edge smooth (Fig. 80: me). Ctenidium (Figs. 79, 80: ct) extending from near mantle margin to rear of mantle cavity; leaflets broadly triangular with narrow, projecting apices. Osphradium (Figs. 79, 80: os) smooth, long, narrow, slightly less than half of ctenidium in length, in shallow depression.

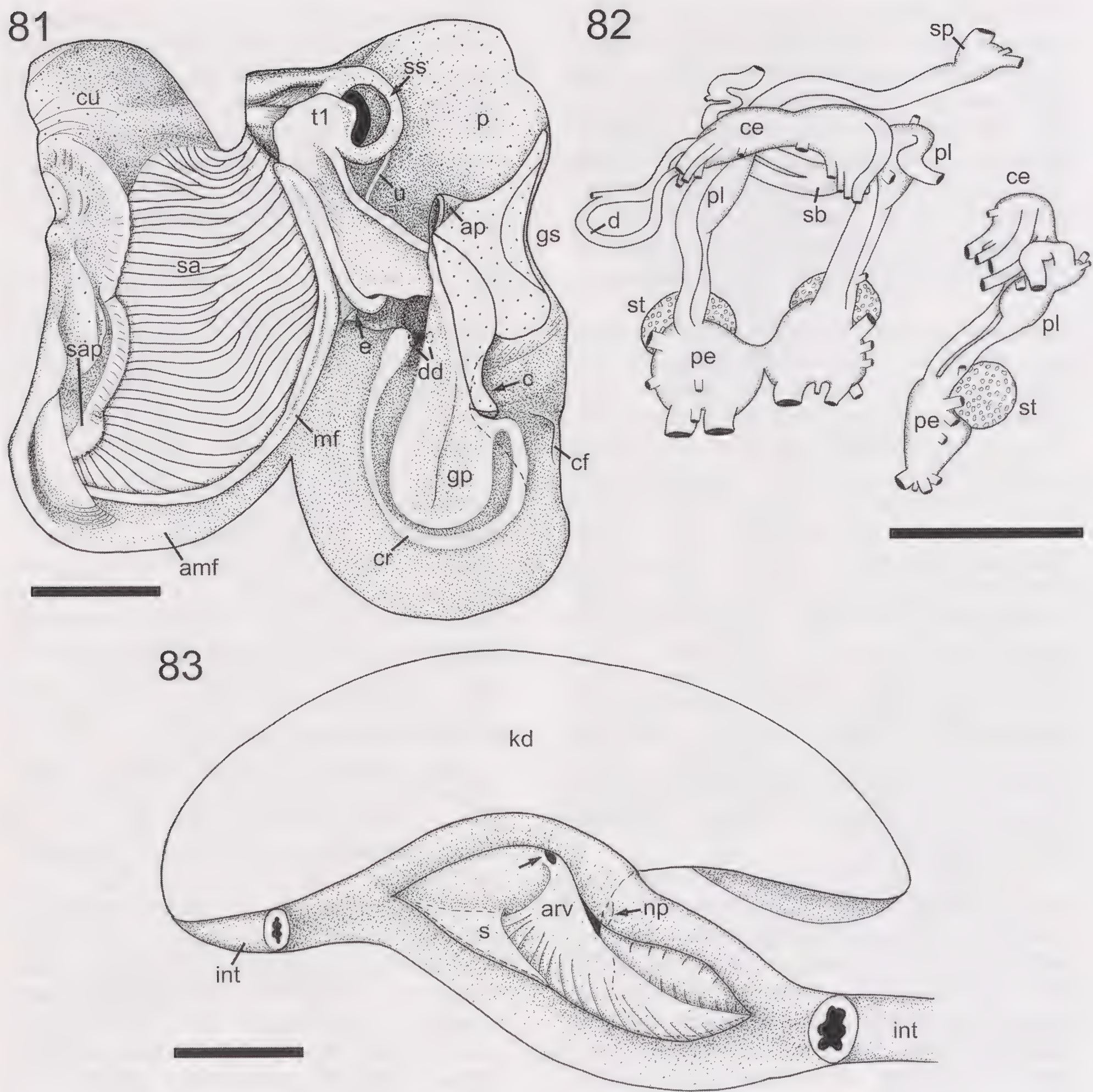
Alimentary System: Foregut. Radula taenioglossate (Fig. 73). Rachidian (Fig. 74) rectangular, wider than tall, with lower margin tapering to narrow, v-shaped projection. Upper margin slightly concave, with cutting edge with single, prominent, pointed central cusp bounded by two to seven fine, pointed denticles on each side (Fig. 75). Lateral teeth with extremely long lateral extensions (Fig. 73), roughly 2.5 length of cutting edge. Cutting edge with single, prominent pointed cusp flanked by two to four inner and 10–12 outer pointed denticles. Marginal teeth (Figs. 73, 76) long, slender, with narrow, elongate, rounded tips bearing ~13–16 fine, rounded denticles of similar size and shape around tip and along distal one fourth of inner edge. Number of denticles on all teeth variable between individuals.

Mouth opening ventrally at anterior end of snout. Buccal mass (Fig. 80: bm) narrow, elongate; small odontophore occupying posterior half of buccal cavity. Narrowly triangular, glandular subradular organ extending along floor of buccal cavity at anterior end of odontophore. Small, paired jaw dorsally flanking mouth at anterior ends of dorsal folds. Shallow, nonglandular buccal pouches extending underneath dorsal folds adjacent to buccal ganglia at rear of buccal cavity. Salivary glands (Fig. 80: sg) forming short, slightly undulating simple tubules, opening dorsolaterally alongside odontophore; salivary glands just passing through circumesophageal nerve ring (Fig. 80: nr) but not extending posteriorly. Thick buccal retractors (Fig. 80: rt) extending from rear wall of buccal mass, inserting on lateral walls of cephalic hemocoel anterior to nerve ring. Nerve ring lying short distance back from posterior end of cephalic tentacles. Radular sac short, projecting slightly past end of buccal mass and curving dorsally underneath anterior esophagus. Within anterior esophagus, tall, glandular midventral fold just behind odontophore. Paired ventral

longitudinal folds commencing immediately behind midventral fold. Walls of anterior and midesophagus with paired, longitudinal ventral and dorsal folds; dorsal and ventral folds continuing through midesophagus and continuous with folds in posterior esophagus. Posterior esophagus with numerous folds of equal height. Midesophageal gland lacking.

Midgut. Best available specimen not well preserved. Esophagus opening to gastric chamber floor at left (Fig. 81: e). Marginal fold (Fig. 81: mf) extending anteriorly alongside major typhlosole (Fig. 81: t1), then turning posteriorly bordering edge of sorting area (Fig. 81: sa). Sorting area rectangular, with rounded posterior margin. Marginal fold elaborated into small, elongate pad at left, posterior tip of sorting area (Fig. 81: sap). Accessory marginal fold (Fig. 81: amf) obsolete anteriorly, curving anteriorly around posterior end of sorting area, bifurcate posteriorly. Midgut roof at left of sorting area cuticularized (Fig. 81: cu). Gastric shield (Fig. 81: gs) large, continuous with cuticle of midgut roof and crystalline style pocket (Fig. 81: p). Thin, weakly developed fold bounding u-shaped depression (Fig. 81: u) below lip of style sac (Fig. 81: ss). Glandular pad (Fig. 81: gp) large, elongate, broadly rounded; accessory pad present at left, anterior tip (Fig. 81: ap). Crescentic ridge (Fig. 81: cr) extending back from near esophageal aperture and fusing to right side of glandular pad, bounding shallow crescentic groove. Proximal crescentic ridge bounding deep pouch with two digestive gland ducts (Fig. 81: dd). Shallow, elongate caecum (Fig. 81: c) extending ventrally under glandular pad behind gastric shield. Single, weakly developed longitudinal fold (Fig. 81: cf) behind gastric shield, opposite caecum. Style sac (Fig. 77: ss) communicating proximally with intestine (Fig. 77: int). Crystalline style present.

Hindgut. Proximal intestine (Fig. 77: int) passing below distal tip of style sac, then extending posteriorly alongside style sac (Fig. 77: ss), forming broad loop over proximal style sac adjacent to main gastric chamber (Fig. 77: sto). Intestine continuing forward, passing under posterior end of main kidney chamber (Fig. 77: kd), entering pallial roof between bladder (Figs. 79, 80: b) and main kidney chamber, to papillate anus near mantle margin (Fig. 80: int).



FIGS. 81–83. Internal anatomy of *Paramelania iridescens* (ZMB 220.037). FIG. 81: Midgut anatomy. Dorsal view, anterior is uppermost; FIG. 82: Circumesophageal nerve ring. Frontal view (left) and left lateral view (right); FIG. 83: Kidney anatomy. Internal view of bladder. Lateral view, anterior is at right. Roof of bladder (below intestine) cut open to reveal interior. Abbreviations: amf, accessory marginal fold; ap, accessory pad; arv, afferent renal vessel; c, caecum; ce, cerebral ganglion; cf, caecal fold; cr, crescentic ridge; cu, cuticularized region in midgut roof; d, dialyneury; dd, digestive gland duct; e, esophagus; gp, glandular pad; gs, gastric shield; int, intestine; kd, kidney; mf, marginal fold; np, nephropore; p, crystalline style pocket; pe, pedal ganglion; pl, pleural ganglion; s, septum; sa, sorting area; sb, subesophageal ganglion; sap, sorting area pad; sp, supraesophageal ganglion; ss, style sac; st, statocyst; t1, major typhlosole; u, u-shaped fold. Scale bars = 1 mm.

Reno-Pericardial System: Voluminous kidney (Fig. 77: kd) extending from anterior end of main gastric chamber (Fig. 77: sto) alongside style sac and pericardium into mantle roof. Kidney lumen partially subdivided into two main chambers. Main chamber (Figs. 77,

83: kd) extending full length of kidney, surrounding pericardium dorsally and at right, anteriorly overhanging base of mantle cavity; lumen mostly occluded by excretory tubules developed in roof and along walls. Large bladder (Figs. 79, 80: b) at right of main

chamber, extending into pallial roof between intestine (Fig. 79: int) and pallial gonoduct (Fig. 79: pr). Bladder (exposed chamber in Fig. 83) communicating with main chamber via small aperture (Fig. 83: arrow) just behind afferent renal vessel (Fig. 83: arv). Bladder partially subdivided posteriorly by incomplete horizontal septum of excretory tissue (Fig. 83: s). Large sheet of excretory tubules branching from afferent renal vessel and extending anteriorly along bladder floor, partially separating shallow ventral chamber below. Nephridial gland absent.

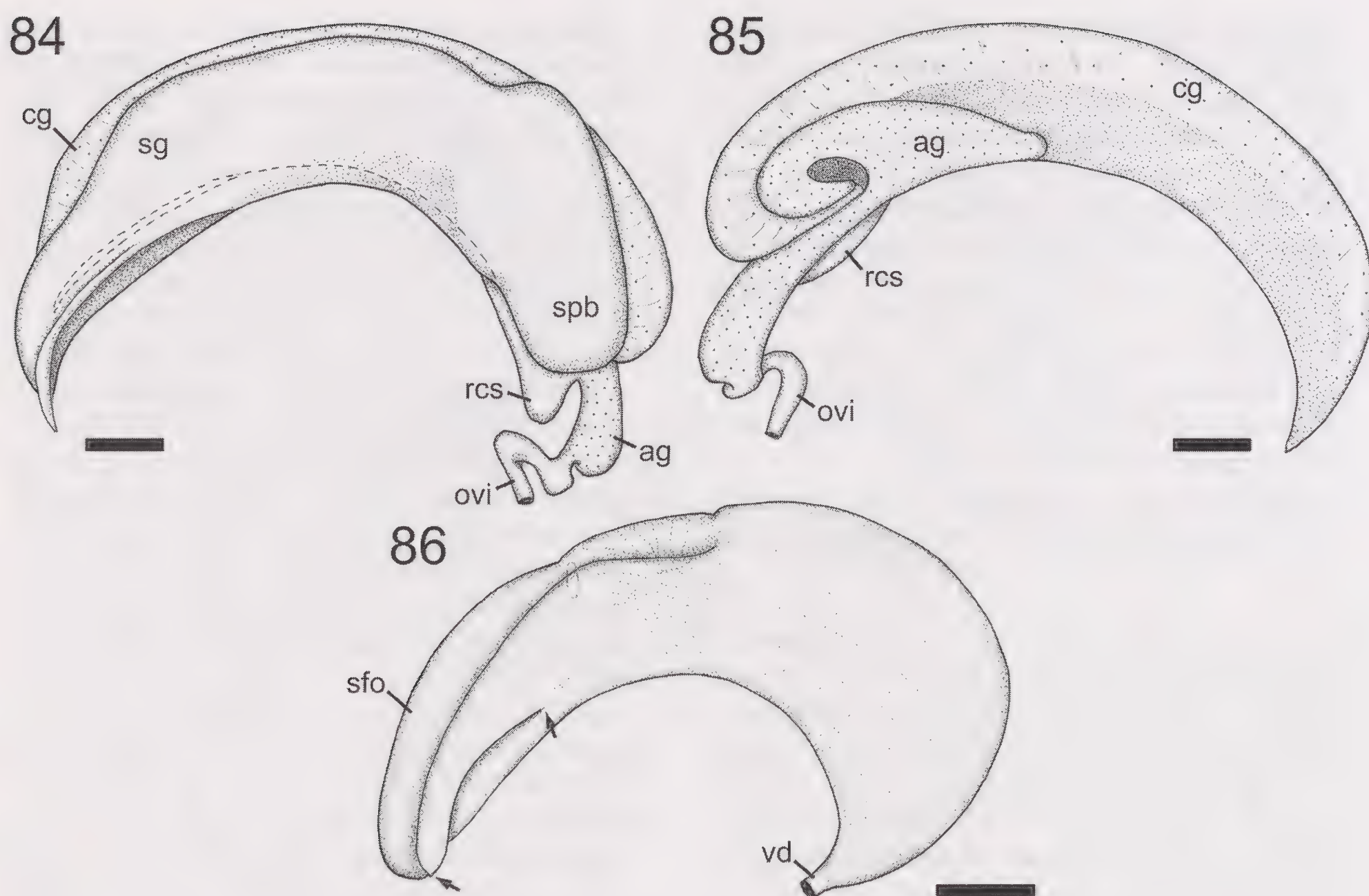
Narrow, deep pericardium (Fig. 77: per) extending underneath kidney alongside style sac (Fig. 77: ss) to intestinal loop.

Nervous System: Cerebral ganglia (Fig. 82: ce) separated by slight constriction, each ganglion producing six to seven nerves (optic, statocyst, tentacular, and three to four labial nerves). Buccal ganglia lying ventrolaterally at base of buccal mass, adjacent to retractor muscles, at outer edges of anterior esophagus. Pleural ganglia (Fig. 82: pl) lying behind and below cerebral ganglia connected to cerebral ganglia by short, thick connectives. Pedal ganglia (Fig. 82: pe) with two prominent anterior nerves and approximately four to five smaller accessory nerves. Statocysts (Fig. 82: st) with numerous angular statoconia present dorsally alongside pedal ganglia behind pedal connectives. Subesophageal ganglion (Fig. 82: sb) separated from left pleural ganglion by slight constriction. In addition to connectives to left pleural and visceral ganglia, subesophageal ganglion producing two stout nerves, one of which forming dialyneurous connection with pallial nerve from right pleural ganglion (Fig. 82: d). Long connective uniting right pleural and supraesophageal ganglia (Fig. 82: sp), the latter lying at left of midesophagus (Fig. 80: sp). Dialyneury formed between pallial nerve of left pleural ganglion and osphradial nerve of supraesophageal ganglion at junction of mantle roof and floor. Single visceral ganglion present at base of cephalic hemocoel.

Female Reproductive System: Gonad (Figs. 77, 79: te) dorsally overlying digestive gland (Fig. 79: dg) from tip of visceral mass to posterior end of gastric chamber (Fig. 79: sto). Oviduct emerging ventrally from ovary. Renal oviduct (Figs. 84, 85: ovi) forming short recurvent loop behind mantle cavity before

entering base of glandular oviduct. Pallial oviduct, with proximal albumen (Figs. 84, 85: ag) and distal capsule glands (Figs. 84, 85: cg). Albumen gland forming rear-facing c-shaped tube at posterior end of pallial oviduct; capsule gland developed along dorsal crest of pallial oviduct. Glandular tissue of capsule and albumen glands with opposing flattened surfaces bounding morphologically dorsal gonoductal groove. Narrow vagina along anterior one third of oviduct opening to sperm gutter (Fig. 84: sg) in median lamina. Gutter leading posteriorly to elongate, broad spermatophore bursa (Fig. 84: spb). Inner wall of median lamina fusing to outer wall, restricting communication between spermatophore bursa and ventral channel to elongate, anterior slit (Fig. 84: double dashed line). Ventral edge of median lamina inner wall (Fig. 84: single dashed line) continuing posteriorly as shallow groove above ventral channel, posteriorly enclosing entrance to seminal receptacle (Figs. 84, 85: rcs). Communication between sperm gutter and ventral channel bounded by two folds: one prominent dorsal fold along outer ventral edge of median lamina inner wall, and one prominent ventral fold extending along ventral edge of vagina. Dorsal and ventral fold fusing posteriorly and rapidly becoming obsolete.

Male Reproductive System: Narrow vas deferens (Fig. 86: vd) emerging ventrally from testes (Figs. 77, 79: te), entering posterior end of prostate at base of mantle cavity. Short distal portion of vas deferens thickened and forming straight seminal vesicle. Prostate glandular, forming flattened tube, opening to mantle cavity through narrow, ventral slit along anterior one third (arrows). Posterior half of prostate separated from anterior half by slight dorsal constriction. Glands of posterior lateral lamina deeply longitudinally grooved; anterior portion of lateral lamina with deep, oblique, rear-facing ledge extending ventrally from dorsal constriction to above aperture. Deep grooves from posterior lateral lamina continuous under ledge, toward aperture of spermatophore forming organ. Posterior medial lamina more weakly longitudinally grooved; anterior medial lamina rather smooth. Dorsal, anterior portion of prostate forming elongate, glandular, tube-like spermatophore-forming organ (Fig. 86: sfo). Organ terminating blindly anteriorly, communicating posteriorly with gonoductal groove via narrow aperture.



FIGS. 84–86. Reproductive anatomy of *Paramelania iridescens* (ZMB 220.099, except when noted). FIG. 84: External, left lateral view of pallial oviduct. Anterior is at left; FIG. 85: External, right lateral view of pallial oviduct. Anterior is at right; FIG. 86: External, left lateral view of prostate (ZMB 220.037). Anterior is at left. Arrows indicate extent of opening to gonoductal groove. Prominent grooves of lateral lamina seen by transparency. Abbreviations: ag, albumen gland; cg, capsule gland; ovi, renal oviduct; rcs, seminal receptacle; sfo, spermatophore forming organ; sg, seminal groove; spb, spermatophore bursa; vd, vas deferens. Scale bars = 1 mm.

Remarks: Moore (1899b) described the anatomy of *Paramelania iridescens* (as *Bythoceras iridescens*) and correctly pointed out the very different anatomical features as compared to *Lavigeria* (as *Nassopsis*) despite similarity in shell form. Among the features described by Moore (1899b) include the short radular sac and small buccal mass, the presence of a crystalline style and two digestive gland ducts. He stated the salivary glands were similar to those of *Tiphobia*, which he incorrectly described as long and branched (Moore, 1898). He correctly likened the nervous system to that of *Tanganycia* (among others), characterized in particular by dialyneury on the right. He compared the radular dentition to the Melanio-planaxoid type (Moore, 1899a) in determining the affinities to be cerithioid (near *Cerithium* and *Tympanotonus*). Although not stated explicitly in the text, the figure appears to show a rachidian with $\sim 5/1/\sim 5$; lateral teeth with $2/1/\sim 6$; similar marginal teeth with $\sim 7/\sim 9$. The spermatophore forming organ was

considered to be lacking by Moore (1899b), who had described the structure as a penis in *Tiphobia* (Moore, 1898) (see also Strong & Glaubrecht, 2002).

Leloup (1953) also provided some information on the operculum and radula with a rachidian broader than tall with $5-6/1/5-6$; lateral teeth with $2/1/8-9$; similar marginal teeth, each with 6–9 denticles. West & Cohen (1996) reported three layers of crossed lamellar microstructure in the shell. As discussed by Glaubrecht (2008), Brown (1994) reported that females of the genus may be ovoviviparous based on the enlarged lower oviduct figured by Moore (1899b). Despite conchological similarities to the ovoviviparous *Lavigeria*, there is no evidence to suggest that this is true; the present anatomical investigations confirm an oviparous reproductive mode at least for *P. iridescens*. Glaubrecht (2008) provided information on the shell, operculum, radula, external anatomy and ecology (as *P. crassigranulata*). Glaubrecht (2008) indicated

that the radula is similar to that of *Paludomus* and *Cleopatra*, but these latter two taxa possess rachidian and lateral teeth that are not so finely and sharply cusped (the prominent central cusp may be squarish, the denticles are more bluntly rounded and may be more similar in size), and marginals with broad, rounded ends and blunt denticles distributed only at the tips.

DISCUSSION

The overriding impression left by this investigation is of remarkable anatomical similarity despite significant differences in shell morphology (Table 1). Anatomical features among the taxa studied here are broadly similar, with organ systems built upon essentially the same plan; this is particularly evident in comparing anatomy of the radula, midgut, kidney and reproductive systems. *Tiphobia* shares this similarity in organization (Strong & Glaubrecht, 2007), as does *Paramelania*, while being a conchological outlier among this assemblage. Several noteworthy differences in the operculum (concentric), midgut (accessory pad) and nervous system (dialyneurous on the right) of *Paramelania* are also present in *Tanganyicia* and *Tiphobia*. But these likely represent plesiomorphic conditions as they occur in *Paludomus* – a fluviatile member of the Paludomidae distributed in Asia.

As stated above, one of the goals of this study is to explore the anatomical data in light of the results of molecular investigations (West & Michel, 2000; Michel, 2004; Wilson et al., 2004). The main difficulty in attempting to assess affinities of tiphobiines based on anatomical characters is that there are apparently few sources of meaningful variation. For example, many of the anatomical differences evident among the tiphobiines represent autapomorphic modifications that do not provide grouping information (e.g., mantle papillae, egg groove, sac-like spermatophore), are difficult to quantify (shape characters relating to, for example, shape of sorting area, glandular pad, pallial gonoduct), or are highly variable and of limited value in assessing affinities (e.g., tooth denticle number). Some variable features almost certainly reflect differences in size. For example, size of the intestinal loop overlying the style sac seems to be strongly correlated with decreasing animal size among synolopsines (Strong & Glaubrecht, 2008). Consequently, the presence or absence of the

proximal intestinal loop cannot be considered independent evidence of relationship. Other sources of variation likely reflect differences in sexual maturity, at least in part. For example, size of the seminal receptacle and size and shape of the bursa vary to some extent depending on seasonal variations and sexual maturity. Other superficially variable characters likely reflect preservational artifacts. This is certainly true of some of the fine folding patterns within the midgut (u-shaped fold, caecal folds, accessory marginal fold), which can be expected to be sensitive to distortion caused by midgut contents and/or poor preservation.

Despite this caveat, this investigation has revealed several instances of special similarity that may indicate a close relationship between some taxa. For example, *Chytra* and *Limnotrochus* have long been considered to be allied (Digby, 1902; Pilsbry & Bequaert, 1927), but united by features that are not necessarily unique, such as the operculum, radula and oviparous reproductive mode. The present analysis has revealed that *Chytra* and *Limnotrochus* also share features of the salivary glands (branching) and spermatophore bursa (long, broad; elongate fold above ventral channel absent). Aspects of the ovipositor pore (u-shaped lumen), esophagus (dorsal and ventral folding patterns) and spermatophore bursa (elongate fold above ventral channel present) are shared only by *Bathanalia* and *Mysorelloides* within this assemblage, but are not necessarily unique among lake taxa (e.g., ovipositor with a u-shaped lumen – *Syrnolopsis lacustris*; esophageal folding patterns – *Potadomoides*; fold in spermatophore bursa – *Cleopatra*).

Tiphobia possesses a complex mixture of features that are shared with various subsets of tiphobiine taxa, including tubular salivary glands (*Bathanalia*, *Mysorelloides*, *Paramelania*), continuous dorsal and ventral folds in the midesophagus (*Chytra*, *Limnotrochus*, *Paramelania*), and a short, narrow spermatophore bursa (*Chytra*, *Limnotrochus*). No unique anatomical features were found that support the suggested affinity between *Tiphobia* and *Bathanalia* based on their spiny shells and misconception of an ovoviviparous reproductive mode in the latter (see Remarks, Table 1).

In addition, unlike several well characterized subsets of paludomids [e.g., *Lavigeria* plus *Potadomides* (Glaubrecht & Strong, 2007); *Syrnolopsini* (Strong & Glaubrecht, 2008)], no unique character was found that is shared by all tiphobiines. The aforementioned similarities in

TABLE 1. Summary of major morphological differences. As in the text, formula for radular tooth descriptions is as follows: (1) rachidian: number of denticles on left side/median cusp/number of denticles on right side, (2) lateral teeth: inner denticles/pronounced cusp/outer denticles, (3) marginal teeth: number of denticles on inner marginal tooth/number of denticles on outer marginal tooth. Spermatophore data from Glaubrecht & Strong (2004); data for *Tiphobia horei* from Strong & Glaubrecht (2007). * – umbilicus present in juveniles of *T. horei*; NA – inapplicable features of the ovipositor in ovoviparous *T. horei*. Abbreviations: ct, ctenidium; nr, circumesophageal nerve ring; ss, style sac; vc, ventral channel.

	<i>Bathanalia</i> <i>straeleni</i>	<i>Chytra</i> <i>kirkii</i>	<i>Limnotrochus</i> <i>thomsoni</i>	<i>Mysorelloides</i> <i>multisulcata</i>	<i>Paramelania</i> <i>iridescens</i>	<i>Tiphobia</i> <i>horei</i>
Shell						
Umbilicus	Present	Present	Present	Present	Absent	Absent*
Layers crossed lamellar structure	2	3	4	3	4	2
Prominent keel	Present	Present	Present	Absent	Absent	Present
External Anatomy						
Operculum (whorls)	Spiral (6)	Spiral (5.5)	Paucispiral (4.5)	Spiral (5)	Concentric, spiral nucleus	Concentric, spiral nucleus
Ovipositor pore	U-shaped	Simple	Simple	U-shaped	?	NA
Egg groove from pore to foot sole	Present	Absent	Absent	Absent	Absent	NA
Hypobranchial gland	Thick	Thin	Thin	Thin	Moderate	Thin
Mantle edge	Papillate	Smooth	Smooth	Smooth	Smooth	Smooth
Osphradium length	~One third ct	~One fourth ct	~One third ct	~Two thirds ct	~One half ct	~One third ct
Alimentary System						
Rachidian	Rectangular/elongate	Squarish	Rectangular/elongate	Rectangular/elongate	Rectangular/broad	Rectangular/elongate
Rachidian denticles	?	6–8/1/6–8	9–13/1/9–13	6–14/1/6–14	2–7/1/2–7	8–15/1/8–15
Lateral denticles	?	5–7/1/9–14	6–7/1/16–20	5–7/1/17–23	2–4/1/10–12	3–6/1/5–16
Marginal denticles	?	~5/~7	~28–32/~28–32	~20–25/~30–35	~13–16/~13–16	5–8/1–3
Outer edge of outer marginal	?	Smooth	Smooth	Cusplate	Smooth	Smooth

(continues)

(continued)

	<i>Bathanalina straeleni</i>	<i>Chytra kirkii</i>	<i>Limnotrochus thomsoni</i>	<i>Mysorelloides multisulcata</i>	<i>Paramelania iridescens</i>	<i>Tiphobia horei</i>
Dorsal/ventral folds in midesophagus	Fusing	Continuous	Continuous	Fusing	Continuous	Continuous
Salivary glands	Tubular	Branching	Branching	Tubular	Tubular	Tubular
Salivary gland position	Through nr	Through nr	Through nr	Through/by-pass nr	Through nr	Through nr
Accessory pad	Absent	Absent	Absent	Absent	Present	Present
Caecal folds	1	1-2	1	1	1	1
Caecum	Present	Present	Present	Absent	Present	Present
U-shaped fold	Present	Absent	Present	Present/Absent	Present	Present
Proximal intestine loop overlying ss	Absent	1 large	1 large	1 small	1 large	2 large
Nervous System						
Cerebral nerves	6	6	6	6	6-7	7
Accessory pedal nerves	5	7-8	6	5-7	4-5	6
Subesophageal nerves	3	5	4	5	2	2
Dialyneury/ zygoneury	Zygoneury	Zygoneury	Zygoneury	Zygoneury	Dialyneury	Dialyneury
Supraesophageal connective	Long	Very long	Long	Long	Long	Long
Reproductive System						
Spermatophore bursa	Long, broad	Short, narrow	Short, narrow	Long, broad	Long, broad	Short, narrow
Connection between bursa and vc	Long	Medium, anterior	Short, anterior	Short, anterior	Medium, anterior	Short, anterior
Prominent fold in bursa above connection to vc	Present, continuous posteriorly	Absent	Absent	Present, continuous posteriorly	Present anteriorly above connection to vc only	?
Spermatophore organ	?	Short	?	Short	Elongate	Elongate
Spermatophore	?	Bifurcate, spines	Simple sac	Bifurcate, spines	Bifurcate	Bifurcate

midgut, gonoduct and kidney organization are also present in *Tanganyicia* (Strong & Glaubrecht, 2002) and may be plesiomorphic among Lake Tanganyika paludomids. The significance of these similarities and differences is not yet clear and several possibilities seem most likely: (1) this assemblage may comprise a paraphyletic grade, (2) in the context of a global phylogeny including all taxa, and all available morphological and molecular evidence, monophyly of the Tiphobiini may nevertheless obtain, supported by at least some of the similarities in organization, (3) this grade or clade also includes *Tanganyicia*, although molecular data have consistently placed it apart. These hypotheses remain to be tested.

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RESEARCH NOTES

SIBLING CANNIBALISM IN JUVENILES OF THE MARINE GASTROPOD *NASSARIUS FESTIVUS* (POWYS, 1835)

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INTRODUCTION

Shell-boring predation is well-studied in the prosobranch gastropods, including representatives of the Naticidae (Carriker, 1981; Kabat, 1990), Muricidae (Carriker, 1981), Buccinidae (Peterson & Black, 1995), Marginellidae (Ponder & Taylor, 1992; Taylor, 1998), and Cassidae (Hughes & Hughes, 1981). In contrast, representatives of the Nassariidae had not been found to bore into shells until Morton & Chan (1997) presented the first evidence of shell-boring predation by *Nassarius festivus* juveniles. Representatives of the Nassariidae are considered to be “the closest attempt of an obligate scavenging life style,” although members, including *Bullia digitalis* and *Ilyanassa obsoleta*, eat live prey (Britton & Morton, 1994). The findings of Morton & Chan (1997) were intriguing because the *N. festivus* adults are not shell borers, but scavengers, which descend readily and speedily on fresh carrion (Morton & Yuen, 2000), whereas the juveniles bore holes and cannibalize their siblings.

Offspring cannibalism of viable siblings in the study of trophic eggs has attracted much attention in such diverse taxa as sharks, non-social insects, frogs, spiders, and prosobranch gastropods (reviewed by Perry & Roitberg, 2006). For example, the sea whelk *Hemifusus tuba* feeds on trophic eggs, resulting in only a mean of 8.8 emerged as juveniles from a mean of 1,500 eggs laid in each capsule (Morton, 1987). Relatively little information is available on the gastropod juveniles that cannibalize similar-sized siblings. The aim of the present study is to provide empirical evidence of sibling cannibalism in *N. festivus* juveniles. The findings of Morton & Chan (1997) were obtained in a wholly accidental manner; some newly metamorphosed *N. festivus* left over an extended public holiday were dead and had their shells bored. The present study also answers the question of whether cannibalism was invoked by hunger.

MATERIALS AND METHODS

Collection and Maintenance of Experimental Animals

Approximately 100 adult *Nassarius festivus* (mean shell length $\pm$ SD: 7 ± 2 mm) were collected from a sandy shore at Lok Wo Sha, Tolo Harbour, Hong Kong (22°20'N, 114°10'E). Upon return to the laboratory, the adult gastropods were kept in a 13 l-fiberglass tank with well-aerated natural seawater of 33‰ salinity. Adults, egg capsules and larvae were maintained at 28°C, the measured temperature at the collection site. The clam *Tapes philippinarum* was opened and offered as food to the adult gastropods every other day. This food ration was shown to be able to maximize egg production (Cheung & Lam, 1999).

Egg capsules deposited on the aquarium wall were transferred to and maintained in a 1 l-glass beaker with 500 ml seawater. Membrane-filtered (pore size: 0.22 μ m) natural seawater (salinity 33‰) was used to maintain egg capsules and larvae and in the experimental procedures. Subsequently, hatched larvae were transferred to a 1 l-glass beaker and reared in seawater on a diet of the alga *Thalassiosira pseudonana* at 2×10^4 cells ml⁻¹ (Pechenik & Fisher, 1979). The antibiotics streptomycin and penicillin G were added at a concentration of 50 μ g ml⁻¹ each to control bacterial growth (Rittschof, 1984). The seawater was changed daily. Larvae that had completed metamorphosis and developed into crawling juveniles (characterized by a pair of tentacles and the resorption of vela) were removed from the glass beaker.

Experiment 1: Starvation

Sixty individuals that had metamorphosed on the same day were used in Experiment 1. Each newly metamorphosed individual was reared in a polystyrene Petri dish with 30 ml seawater

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renewed daily. There were two treatments. Three groups, each with ten individuals, were assigned to each of the two treatments as replicates. In the fed control groups, the juveniles were fed to satiation with *T. philippinarum* tissue daily; in the unfed groups, the juveniles were starved throughout the whole experimental period. The juveniles were examined every day, and those that did not respond to the stimulation of a pointed tip were considered dead. The experiment ended when all of the juveniles in the unfed treatment had died, at day 28 post-metamorphosis.

Experiment 2: Cannibalism

Similar to Experiment 1, 60 individuals that had metamorphosed on the same day were used in Experiment 2, also with two treatments and three replicate groups, each with ten individuals. Ten newly metamorphosed individuals in a group were, however, reared together in a polystyrene beaker with 300 ml seawater, renewed daily. Individuals in the fed control and unfed treatments received the same feeding or starving regimes as those in Experiment 1.

The shell length of each individual was measured every three days (e.g., on days 1, 4, 7 post-metamorphosis) under a stereoscopic microscope equipped with an eyepiece graticule at a magnification of 40X. As in Experiment 1, the juveniles were examined daily, and those that did not respond to the stimulation of a pointed tip were considered dead. Empty shells that appeared were collected and fixed with 4% (v/v) formaldehyde in autoclaved filtered seawater for further examination (i.e., whether they were intact, broken in half or in smaller pieces, or with a borehole). The experiment ended at day 28 post-metamorphosis.

Statistical Analysis

The normality of the data and homogeneity of variances were checked with Kolmogorov-Smirnov test and Barlett's test, respectively. Median lethal time (LT_{50}) was calculated for each replicate group using Probit analysis. Shell length data of all juveniles in a replicate group were first pooled together. T-tests were used to compare the mean LT_{50} and mean time for the first appearance of mortality of the unfed juveniles in Experiments 1 and 2 ($df = 4$ for all cases). The juvenile growth rates were compared using ANCOVA. The statistical tests were performed using the statistical software SPSS 11.0.

RESULTS

Experiment 1: Starvation

In the experiment in which the juveniles were kept separately, all fed control individuals survived 28 days post-metamorphosis (Fig. 1). In contrast, mortality of the unfed juveniles first occurred on day 8, with the mean time for the first appearance of mortality among the replicates being 12 ± 3.5 days post-metamorphosis (1 SD) ($n = 3$, each with a group of ten juveniles). No unfed juvenile survived beyond day 28. Furthermore, the mean LT_{50} for the unfed group was 16.8 ± 3.5 days post-metamorphosis (1 SD) ($n = 3$, each with a group of ten juveniles).

Experiment 2: Cannibalism

When the juveniles in a replicate were kept together in the same aquarium, all fed control juveniles survived 28 days post-metamorphosis (Fig. 2). In contrast, mortality first occurred on day 3 for the unfed juveniles, with the mean time for the first appearance of mortality among replicates being 3.7 ± 1.2 days post-metamorphosis (1 SD) ($n = 3$, each with a group of ten juveniles). This mean time was significantly shorter than the mean of the unfed group from Experiment 1 ($t_4 = 3.95$, $P = 0.017$). Of the unfed individuals, only 17% survived to the end of the experiment (Fig. 2). Furthermore, the mean LT_{50} for the unfed group was 15.2 ± 3.4 days post-metamorphosis (1 SD) ($n = 3$, each with a group of ten juveniles). This mean was not significantly different from the mean of the unfed group from Experiment 1 ($t_4 = 0.58$, $P = 0.595$).

The control juveniles increased their mean shell length of 0.93 ± 0.03 mm (1 SD) at day 1 to the mean of 2.41 ± 0.33 mm (1 SD) at day 28 post-metamorphosis (in both cases, $n = 3$, each with a group of ten juveniles) (Fig. 3). The unfed juveniles increased their mean shell length of 0.90 ± 0.02 mm (1 SD) at day 1 ($n = 3$, each with a group of ten juveniles) to the mean of 1.33 ± 0.20 mm (1 SD) at days 25 and 28 post-metamorphosis (in both cases, $n = 3$, each with a group of one to three juveniles). The change in the mean shell length of the unfed juveniles between each data point was positive up to day 25 post-metamorphosis (Fig. 3).

Both fed and unfed individuals grew at the same slow rate for the first ten days, to about 1 mm (ANCOVA: $t_{20} = 0.09$, $P > 0.5$). Thereafter they diverged. The fed individuals grew significantly faster than the unfed individuals between days 10 and 28 (ANCOVA: $t_{20} = 9.32$, P

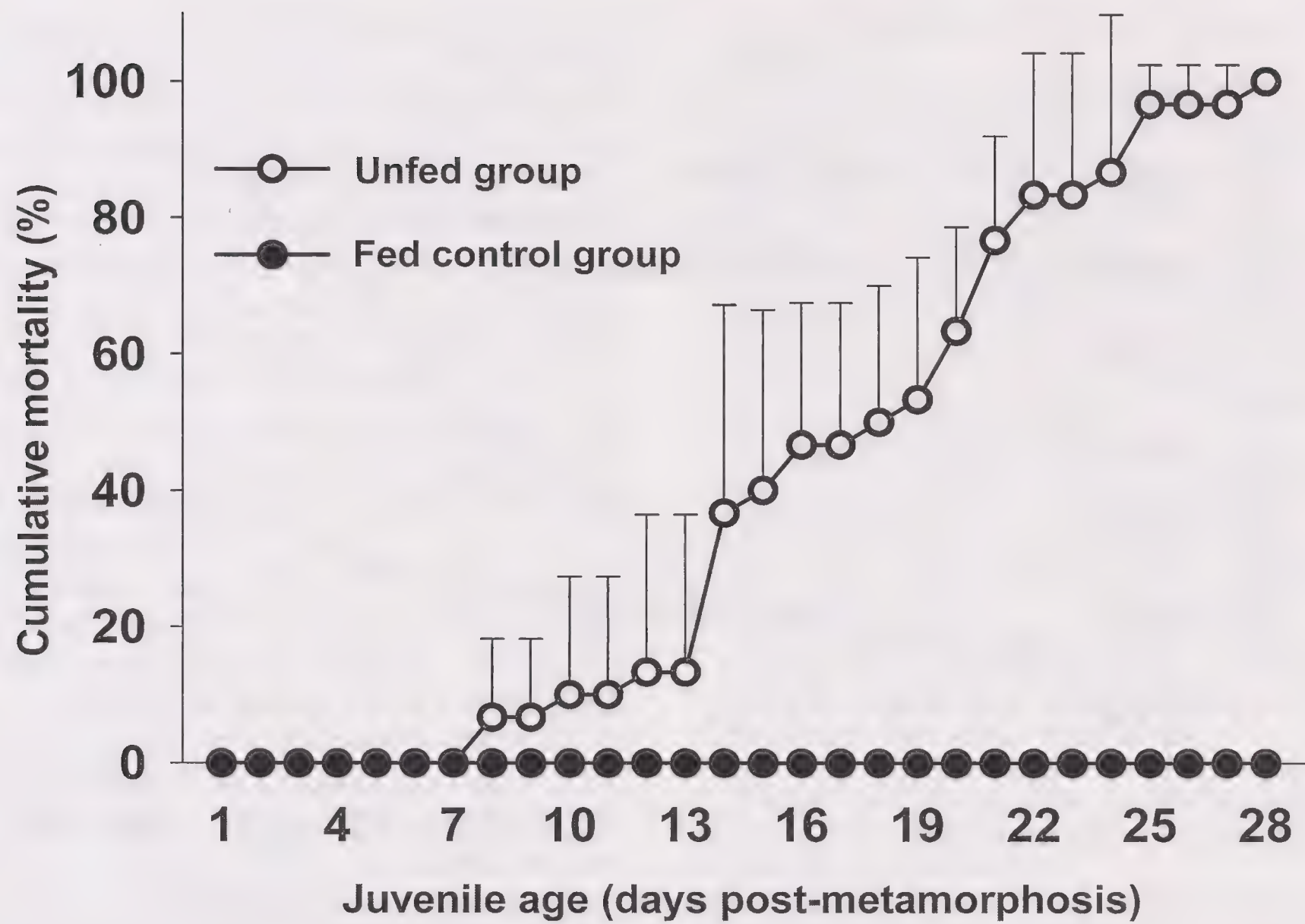


FIG. 1. Experiment 1. Cumulative mortality of fed and unfed *Nassarius festivus* juveniles. Each data point represents the mean (+ SD) of three replicates, each with a group of ten juveniles; juveniles in a replicate were kept separately.

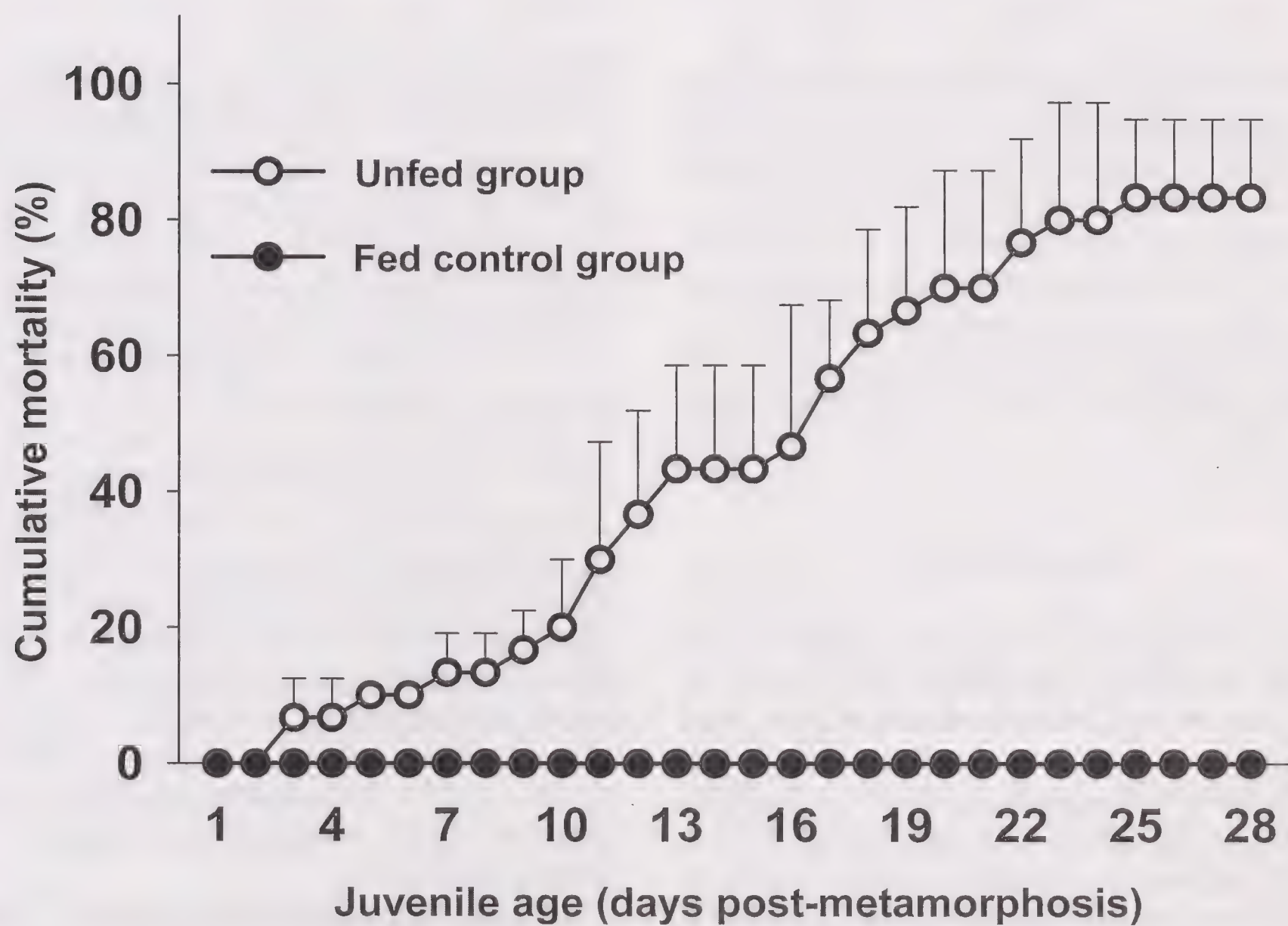


FIG. 2. Experiment 2. Cumulative mortality of fed and unfed *Nassarius festivus* juveniles. Each data point represents the mean (+ SD) of three replicates, each with a group of ten juveniles; juveniles in a replicate were kept together in the same aquarium.

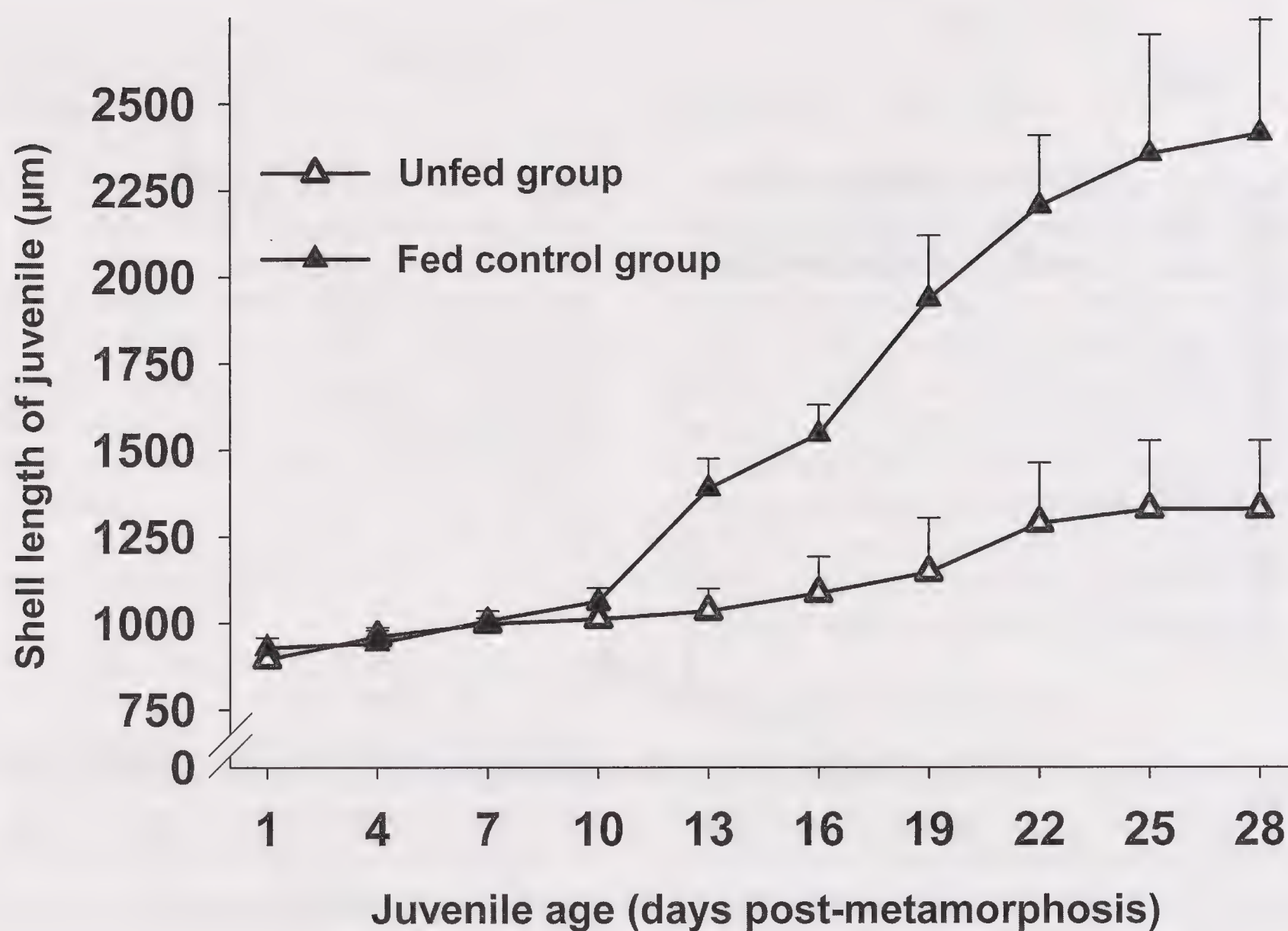


FIG. 3. Experiment 2. Mean shell length of *Nassarius festivus* juveniles. Each data point represents the mean (+ SD) of three replicates, each with a group of one to ten juveniles; juveniles in a replicate were kept together in the same aquarium. The shell lengths of all juveniles in a replicate were first pooled together.

< 0.001). The growth rates of both fed and unfed groups also increased after the first 10 days (fed group – ANCOVA: $t_{29} = 2.05$, $P < 0.05$; unfed group – ANCOVA: $t_{29} = 4.39$, $P < 0.001$).

Among the 25 empty shells of the unfed *N. festivus* juveniles examined, 18 of them had intact shells with no observable damage or scars, three had broken shells in halves or in smaller pieces and four had a borehole on their shells.

DISCUSSION

This present study provides experimental evidence of sibling cannibalism in *Nassarius festivus* juveniles. Firstly, mortality of the unfed juveniles first occurred on day 3 post-metamorphosis when these juveniles were kept together in the same aquarium (the mean time for the first appearance of mortality = 3.7 days; Fig. 2). In contrast, mortality first occurred on day 8 when unfed juveniles were kept separately (the mean time for the first appearance of mortality = 12 days; Fig. 1). These results suggest that mortality due to non-starvation cause, most likely, takes place long before the occurrence

of mortality due to starvation. Secondly, positive growth in the mean shell length of the unfed juveniles up to day 25 post-metamorphosis in Experiment 2 indicates energy gain from cannibalized siblings or sibling carrion (Fig. 3). Thirdly, 17% of the unfed individuals survived to the end of Experiment 2, in which juveniles were kept together, while none survived after the same experimental period in Experiment 1, in which juveniles were kept separately. Survivorship of the unfed individuals was enhanced because of sibling cannibalism. Finally, broken shells, as well as boreholes, were found among the empty shells of these individuals. The unfed juveniles attacked other individuals and broke their shells into two or more pieces in Experiment 2 (personal observation). Results of the present study, along with those of Morton & Chan (1997), demonstrate that at least one member of the Nassaridae engages in shell-boring predation.

The present study also suggests that cannibalism was not a generalized strategy, but invoked only during periods of starvation in the newly metamorphosed *N. festivus*. The well-fed juveniles that were kept together in the same aquarium all survived 28 days post-metamor-

phosis, indicating no mortality due to cannibalism (or any other causes) (Fig. 2). Polis (1981) attributed cannibalism to the unavailability of alternate prey. As predicted by foraging theory, an animal may expand its diet beyond the normal limits of acceptable prey during periods of hunger or limited food (Polis, 1981). This study found that the *N. festivus* juveniles bored holes and cannibalized their siblings when they lacked carrion to scavenge. Fed juveniles did not bore, because clam carrion was readily available and was, thereby, less energy-consuming to obtain. The juveniles might also be injured when they attacked their siblings.

Cannibalism may enhance the survival of an individual during the transition time needed to discover natural prey (Morton, 1987). The present study demonstrates that cannibalism allowed 17% of *N. festivus* juveniles to survive to day 28 post-metamorphosis (in contrast to 0%). The importance of cannibalism as an alternative feeding strategy among these well-known scavengers to their species success or fitness may reflect the fact that carrion is only ephemerally and infrequently available to scavengers (Britton & Morton, 1994). Feeding is further restricted in *N. festivus* as individuals retreat into the sand when tides ebb. Morton (1987) and Dietl (2003) suggested that small population size and dispersal of siblings would, however, make cannibalism an ineffective juvenile survival mechanism because cannibalism may decrease the species success or fitness by removing potential reproductive partners. It is not known if population size and sibling dispersal have been important to the evolution of cannibalism in the Nassariidae. Nonetheless, cannibalism could be an effective mean of persistence during times of low food availability.

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PHYLOGENETIC POSITION OF THE GENUS *CRYPTAZECA* AND THE FAMILY AZECIDAE WITHIN THE SYSTEM OF THE STYLOMMATOPHORA

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INTRODUCTION

The first data about the genus *Cryptazeca* were provided by Folin & Bérillon (1877a) when they described *Azeca monodonta* based on the study of two empty shells collected near Bayonne in southwestern France. Later they collected some live specimens and established the genus *Cryptazeca* for it, after study of its anatomy (Folin & Bérillon, 1877b, 1891). This genus was included together with *Ferussacia*, *Cecilioides*, *Azeca* (with *Hypnophila*), *Cochlicopa*, and five additional genera in the family Ferussaciidae (Pilsbry, 1908). Watson (1928) noticed that *Ferussacia* and *Cecilioides* had a sigmurethrous excretory system and placed them and the family Ferussaciidae in the infraorder Sigmurethra, whereas Steenberg (1925) and Zilch (1959) placed *Azeca*, *Cochlicopa*, and *Hypnophila* in the family Cochlicopidae (infraorder Orthurethra).

New live specimens of the genus *Cryptazeca* were collected in 1987 and its excretory system described as being of the orthurethrous type by Gómez & Angulo (1987). Consequently, these authors proposed to change the taxonomic position of this genus to be placed with *Azeca*, *Cochlicopa*, and *Hypnophila* in the family Cochlicopidae. Detailed anatomical and histological studies of the reproductive system also corroborated the close relationships among *Cryptazeca*, *Azeca*, and *Hypnophila* (Gómez & Angulo, 1987, 1990; Gómez, 1990b, 1991). Nevertheless, Schileyko (1976) considered that orthurethria was probably a primary condition for Stylommatophora, which could be retained in some taxa outside orthurethral groups. This led again to the placement of *Cryptazeca* within the family Ferussaciidae. As a result, the classification followed by the CLECOM project (Bank et al., 2001; Falkner et al., 2001) placed *Cryptazeca* (Cryptazecinae) with *Ferussacia*, *Cecilioides*, and *Hohenwartiana* (Ferussaciinae) within the Ferussaciidae, in the superfam-

ily Achatinoidea. The families Cochlicopidae (genus *Cochlicopa*) and Azecidae (genera *Azeca* and *Hypnophila*) were placed in the Cochlicopoidea. On the other hand, Bouchet & Rocroi (2005) classified *Cryptazeca* with *Azeca* and *Hypnophila* in the Cochlicopidae, subfamily Azecinae (syn. Cryptazecinae), sister group of the Cochlicopinae.

In the present work, we have used molecular phylogenetics to reexamine the relationships of the genus *Cryptazeca* with respect to Ferussaciidae, Cochlicopidae and Azecidae. This study gives additional information about the validity of conchological and anatomical characters in the resolution of the taxonomy of these genera and families. It also allows us to determine whether Azecidae and Cochlicopidae are sister groups and to establish the position of the Azecidae within the suborder Stylommatophora. To allow comparison with Wade et al. (2001, 2006), who provided the most comprehensive molecular study of stylommatophoran relationships, we have used part of the nuclear ribosomal RNA gene cluster.

MATERIALS AND METHODS

Approximately 1,460 nucleotides of the rRNA gene-cluster were amplified for four taxa – *Azeca* (sample locality U.T.M. 30TXN78), *Cryptazeca* (30TXN78), *Ferussacia* (30SYJ02), and *Hypnophila* (30SVF56) – using two overlapping primer sets (Wade et al., 2006); 42 additional sequences were obtained from the GenBank database and included in the phylogenetic analyses (details and GenBank accession numbers given in Table 1). Due to the numerous insertions and deletions characterizing sequences of rRNA genes, any position that could not be reliably aligned was excluded from subsequent analyses.

Phylogenetic trees, incorporating all 46 species, were constructed using both neighbour-

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Species	5.8S ribosomal RNA gene, partial sequence; internal transcribed spacer 2, complete sequence; and 28S ribosomal RNA gene, partial sequence
<i>Albinaria xantostoma</i>	AY014048
<i>Archachatina marginata</i>	AY014070, AY014071
<i>Arion hortensis</i>	AY014143
<i>Azeca goodalli</i> *	FJ791121
<i>Carychium tridentatum</i>	AY014148
<i>Cerastus schweinfurthii</i>	AY014040
<i>Chondrina avenacea</i>	AY014032
<i>Chondrina clienta</i>	AY014031
<i>Cochlicopa lubrica</i>	AY014019
<i>Cochlicopa lubricella</i>	AY014020
<i>Cryptazeca monodonta</i> *	FJ791122
<i>Draparnaudia singularis</i>	AY841290, AY841291
<i>Elasmias luakahaense</i>	AY841280
<i>Eostrobilops nipponica</i>	AY841287
<i>Eua zebrina</i>	AY014046
<i>Ferussacia folliculus</i>	AY841302
<i>Ferussacia folliculus</i> *	FJ791120
<i>Gastrocopta armifera</i>	AY841286
<i>Hypnophila malagana</i> *	FJ791123
<i>Lauria cylindracea</i>	AY014023
<i>Lauria fasciolata</i>	AY014024
<i>Leptachatina lepida</i>	AY014021, AY014022
<i>Luchuena reticulata</i>	AY841288
<i>Macaronapaeus vulgaris</i>	AY014036, AY014037
<i>Mandarina ponderosa</i>	AY841320
<i>Mastus pupa</i>	AY014038, AY014039
<i>Melampus luteus</i>	AY014146
<i>Napaeus pruninus</i>	AY841289
<i>Orcula austriaca</i>	AY014028
<i>Otala lactea</i>	AY841336
<i>Oxychilus alliarius</i>	AY014114
<i>Oxychilus helveticus</i>	AY014115
<i>Pachnodus silhouettanus</i>	AY014041
<i>Partula suturalis</i>	AY014042
<i>Partulina proxima</i>	AY841281, AY841282
<i>Pene sidonensis</i>	AY014035
<i>Pronesopupa acanthinula</i>	AY841285
<i>Pupoides albilabris</i>	AY841283, AY841284
<i>Pyramidula rupestris</i>	AY014029, AY014030
<i>Rumina decollata</i>	AY014065
<i>Samoana conica</i>	AY014045
<i>Solatopupa similis</i>	AY014033
<i>Succinea striata</i>	AY841295
<i>Vallonia costata</i>	AY014025
<i>Vallonia excentrica</i>	AY014026
<i>Vertigo antivergo</i>	AY014027

TABLE 1. Samples and GenBank accession numbers for all the sequences used in the phylogenetic analyses. Asterisks (*) represent the four taxa amplified in this work.

←

joining (NJ) and Bayesian inference (BI). Neighbour-joining analysis (Saitou & Nei, 1987) was carried out using the PAUP* (version 4.0d65) package (Swofford, 2002). Distances were corrected for multiple hits using the general time reversible (GTR) model (Lanave et al., 1984), with between-site rate heterogeneity accounted for by incorporating a proportion of invariant sites (I) and gamma-distributed rates (G) into the model (Gu et al., 1995). The rate matrix, base frequencies, proportion of invariant sites (pinvar), and shape parameter (α) of the gamma distribution were estimated using ModelTest 3.06 program (Posada & Crandall, 1998) according with Akaike Information Criterion (AIC). Support of the recovered NJ tree was evaluated with non-parametric bootstrap proportions (NJ bootstrap – 1,000 pseudoreplicates). BI analysis was performed using the MrBayes version 3.0b4 package (Huelsenbeck & Ronquist, 2001). A GTR + Gamma model was used. This model uses substitutional information only and excludes gaps (Lanave et al., 1984). Rate heterogeneity between sites was accounted for by incorporating invariant sites (I) and gamma-distributed rates (G) into the model (Gu et al., 1995). The tree space was explored using four chains of a Markov Chain Monte-Carlo algorithm for five million generations, sampling every 100 generations. To ensure adequate chain swapping, the heating parameter was set to 0.05. A consensus tree was built using the last 1,000 trees (burn-in = 49,001 samples). Support of the recovered BI trees was evaluated with Bayesian posterior probabilities (BPPs). The non-stylommatophoran pulmonates *Melampus luteus* and *Carychium tridentatum* were used as outgroups.

RESULTS

The consensus alignment of the four new sequences was initially 1,538 bp long and included the 3' end of the 5.8S ribosomal gene (92 bp), the complete ITS-2 region (609 bp), and the partial sequence of the 28S ribosomal gene (approximately 837 bp). Sequence variation at the ITS-2 region was extremely high, and most of its sites could not be aligned when considering all the taxa. Thus, all ITS-2 sites were excluded from the phylogenetic analyses.

The phylogenetic reconstructions were based on a subset of 900 positions (92 positions of the 5.8S and 808 of the 28S). Neighbour-joining and Bayesian phylogenies of the rRNA gene-cluster are given in Figure 1.

The “achatinoid” and “non-achatinoid” clades were recovered as the two basal groups (100% BPP, 100% NJ and 100% BPP, 83% NJ, respectively). Five main phylogroups were obtained within the non-achatinoid clade, including the Elasmognatha, Helicoidea, Clausilioidea, Arionoidea + Limacoidea, and the Orthurethra. As expected, *Ferussacia* belonged to the “achatinoid” clade. Nevertheless, *Cryptazeca* was placed together with *Hypnophila* and *Azeca* in the “non-achatinoid” clade. All these three genera constituted a monophyletic group, the Azecidae, highly supported (100% BPP, 98% NJ). *Cryptazeca* constituted the sister group of *Hypnophila* (94% BPP, 75% NJ). The Azecidae clade was included within the orthurethrous group as an independent lineage. The Orthurethra taxa, including the family Azecidae, formed a monophyletic group only supported by low values in the Bayesian analysis (73% BPP). Three main monophyletic groups highly supported were recovered within the Orthurethra: the Azecidae (100% BPP, 98% NJ), the Chondrinidae (98% BPP, 93% NJ), and a clade joining the rest of the orthurethrous families (100% BPP, 88% NJ). Nevertheless, the phylogenetic relationships of these three basal clades were not fully resolved.

DISCUSSION

Phylogenetic analyses were based on 900 nucleotide positions of the LSU rRNA genes. This number was slightly greater than the 823 nucleotides considered in the work published by Wade et al. (2001, 2006).

The phylogenetic reconstructions clearly demonstrated that *Cryptazeca* is not related with the Ferussaciidae. On the contrary, it was placed far apart from the “achatinoid clade”. This indicated that the elongate, smooth, glass-like, translucent shell, with a pear-shaped aperture, characters that are common to ferussaciids and *Cryptazeca*, are a case of homoplastic combination of characters, and should not be used to join these taxa.

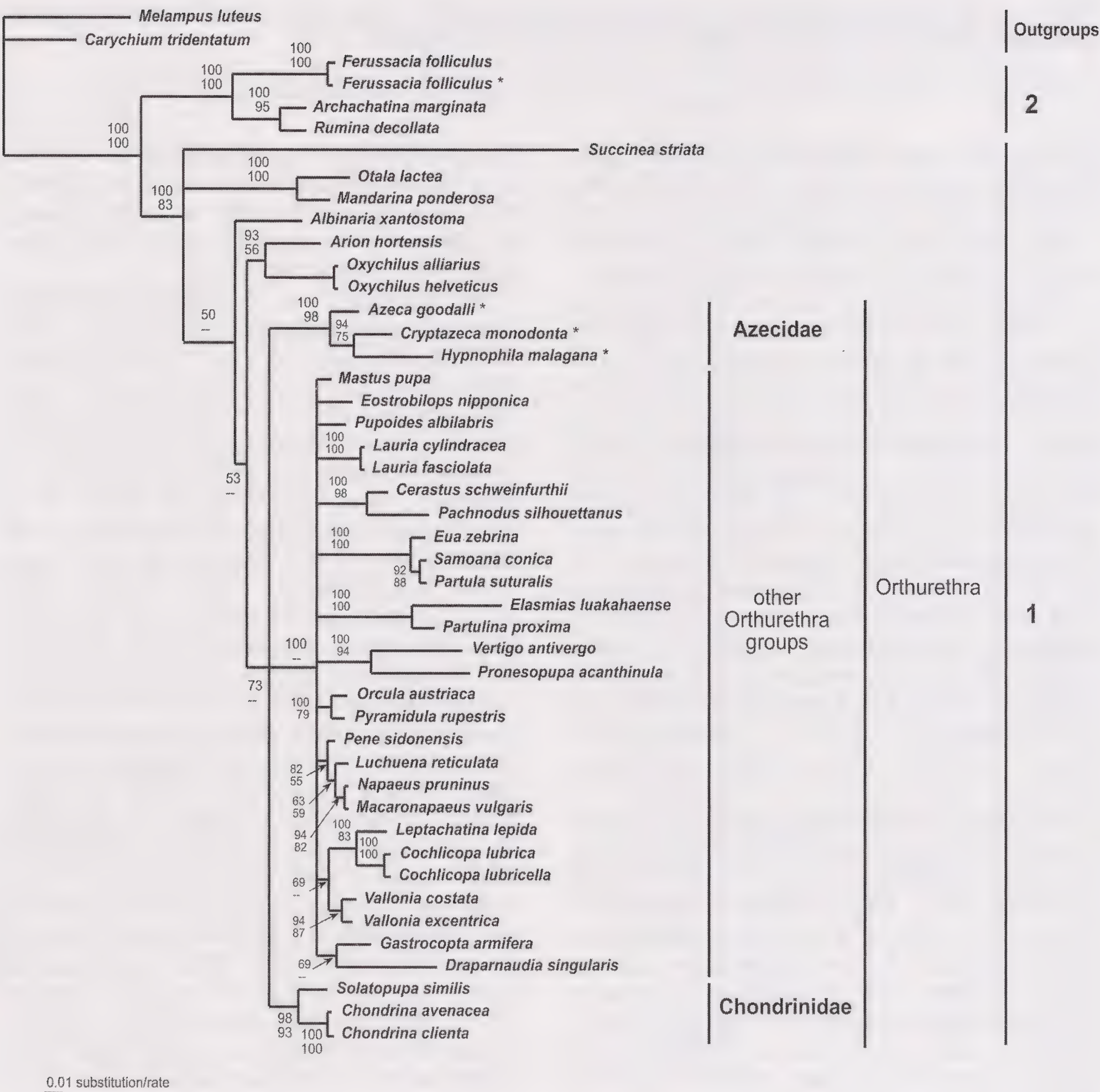


FIG. 1. Phylogenetic relationships (BI phylogram) of *Cryptazeca* and the family Azecidae. Numbers represent support for BI and NJ from top to bottom. Hyphens indicate no support values for NJ. Asterisks (*) represent the four taxa amplified in this work. 1: “non-achatinoid” clade; 2: “achatinoid” clade.

Cryptazeca was recovered as the sister group of *Hypnophila*, as was previously suggested by some authors based on the similarities in shell morphology (Gittenberger, 1983; Gómez & Angulo, 1987), but also by the reproductive system anatomy and shell microsculpture (Gómez & Angulo, 1987; Gómez, 1990a, b). Nevertheless, both genera continued to be classified far apart in different infrasuborders (Schileyko, 1999; Bank et al., 2001) based on some misinterpretations of *Cryptazeca* morphology.

The phylogenetic analyses showed that *Azeca* is closely related to *Cryptazeca* and *Hypnophila*. These three genera constituted a clade that we propose to be called the Azecidae. The subfamily Azecinae was created by Watson (1920) to highlight the anatomical differences that existed between *Azeca* (absence of diverticulum and penial appendix, among other characters) and *Cochlicopa* (with both reproductive organs). The latter genus constituted the subfamily Cochlicopinae in the classification of Watson (1920). Later, some

classifications have considered both taxa as different families (Kennard & Woodward, 1926; Bank et al., 2001). Current classifications consider Azecidae and Cochlicopidae as sister groups, either as subfamilies of one family (Bouchet & Rocroi, 2005) or as families within the same superfamily (Bank et al., 2001). The new phylogenetic evidence demonstrates that Azecidae and Cochlicopidae are not sister groups. According to Wade et al. (2006), *Cochlicopa* is the sister group of *Leptachatina* (Amastridae), within a large monophyletic group that included all the orthurethrous families, with the exception of Chondrinidae. The Azecidae constituted a third independent main group within the Orthurethra clade, and its monophyly was highly supported by both phylogenetic analyses. Here, again, similarities in shell morphology – glossy, translucent, brown, fusiform-oval shells – led to an inaccurate classification for *Azeca* and *Cochlicopa*.

The monophyly of the Azecidae is supported by shell characters (Gittenberger, 1983), including shell aperture and microsculpture (Gómez, 1990a), reproductive system anatomy (Gómez, 1990b, 1991), and molecular data (present work). Shell characters of this family include: pear shaped aperture, with very narrow parieto-palatal border; slightly curved inward palatal lip, slightly narrowing the aperture; continuous peristome with conspicuous parietal callus extending to columellar bottom; presence of aperture denticles, with at least a columellar tooth (sometimes reduced in *Hypnophila*); and microsculpture of spiral lines on the protoconch and teleoconch. The genital system includes a fertilization chamber surrounded by a voluminous gland formed by goblet gland cells (not studied in *Hypnophila*), a blind-ended allospermidut, and a vagina wall with brown pigmentary cells embedded in it (not a vaginal gland as interpreted by other authors). Male distal organs are very simple, excluding the presence of a sarcobellum in *Cryptazeca*.

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THE PROPER NAME FOR THE GEODUCK: RESURRECTION OF
PANOPEA GENEROSA GOULD, 1850, FROM THE SYNONYMY OF
PANOPEA ABRUPTA (CONRAD, 1849) (BIVALVIA: MYOIDA: HIATELLIDAE)

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INTRODUCTION

In 1849, Conrad described, illustrated, and assigned the name *Mya abrupta* to a new species of fossil bivalve collected from Miocene deposits along the banks of the Columbia River near Astoria, Oregon, during the United States Exploring Expedition of 1838–1842 (Conrad, 1849: 723, pl. 17, fig. 5a, b, USNM 3608; Figs. 1–3). Conrad described it as:

“Subelliptical, slightly ventricose, widely gaping posteriorly. Surface marked with concentric undulations. Beaks separated, nearly medial, slightly prominent. Anterior margin acute, orbiculate; posterior margin abrupt, arcuate, somewhat reflexed; basal (inferior) margin arcuate; dorsal margin short, straight, nearly parallel with the base.”

In 1850, Gould described the valves of a new extant species collected from the Nisqually region of Puget Sound, Washington, during the same expedition and assigned it the name *Panopea generosa* (Gould, 1850: 215, USNM 5894; Figs. 4–7). Gould (1852: 385–386; 1860, pl. 34, fig. 507, 507a) later figured and expanded the description:

“Shell large and ponderous, chalky white, of a somewhat quadrilateral form, the basal and hinge margins being nearly parallel; the posterior extremity broadly truncated a very little obliquely, and the anterior extremity broadly rounded; anteriorly it gapes slightly, but posteriorly it gapes broadly, and the valves are here somewhat everted. The surface is coarsely undulated concentrically, and covered by an obliquely, and somewhat plumosely wrinkled, dirty yellow epidermis. The beaks are sharp and prominent, placed near the middle of the superior margin; the anterior umbonal slope is tumid, the posterior a little compressed. The hinge is rather slender, having a single elevated, erect, obliquely triangular tooth in each

valve, with a pit behind that in the right valve, and a crest-like elevation for the attachment of the ligament behind them. Ligament external and double. Cavity of the beaks profound, muscular and pallial cicatrices broad and well impressed; posterior muscular scar but little broader than the pallial impressions; siphonal sinus shallow, small.”

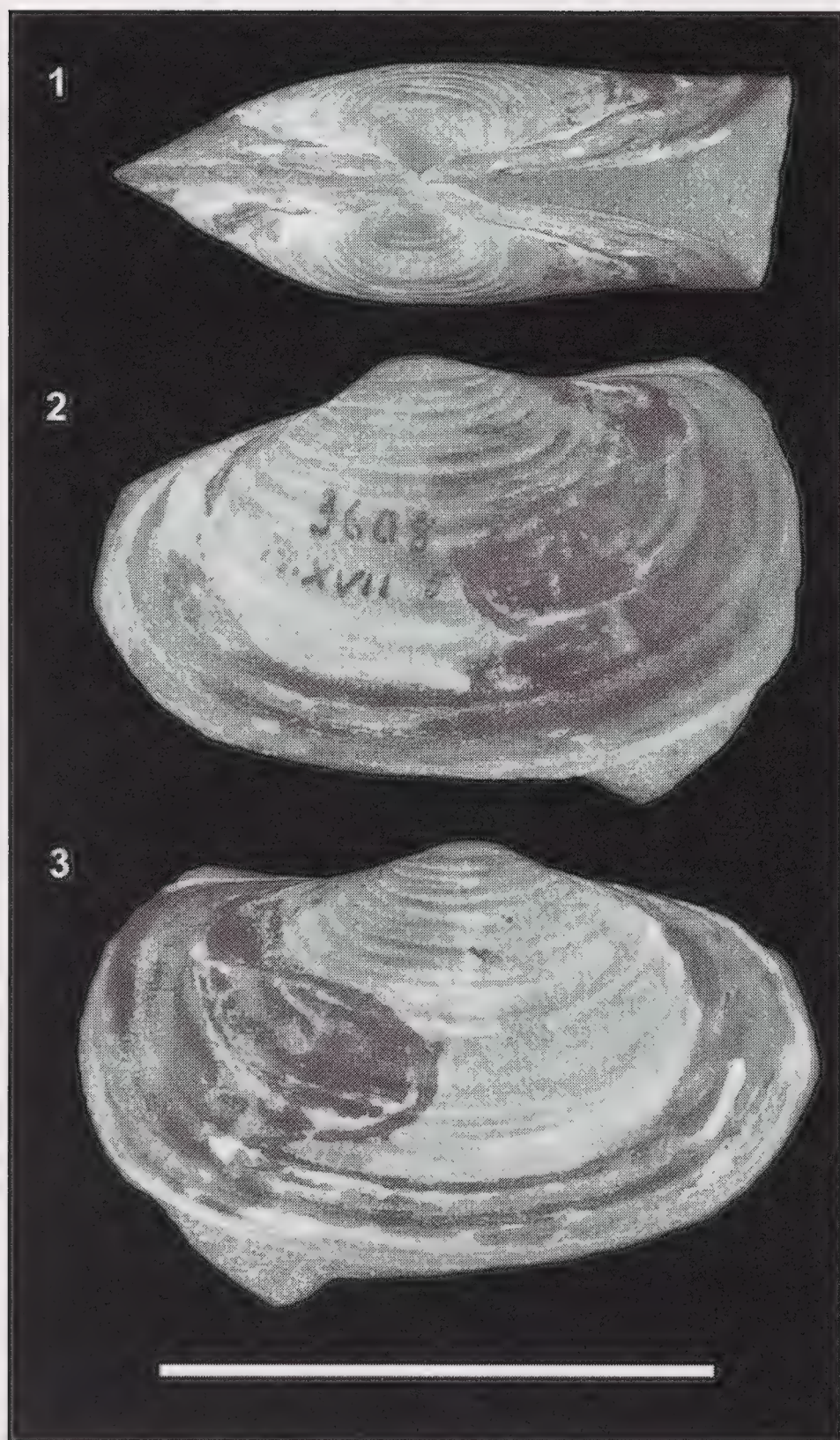
MATERIAL EXAMINED

Holotype of *Mya abrupta*, USNM 3608; holotype of *Panopea generosa*, USNM 5894; *Panopea* spp. (n = 30) in collections of the Burke Museum of Natural History and Culture, University of Washington, Seattle, collected from lower Oligocene to Miocene deposits in Oregon, Washington, and British Columbia, Canada (catalog numbers, some of which include multiple specimens: 04471, 04510, 06650, 06697, 06705, 13348, 13891, 18423, 18892, 18924, 21391, 22341, 24860, 26317, 27512, 27611, 27762, 29556, 42797, 53669, 61705, 73465, 91557, 96501, W485); and more than 4,000 specimens of *Panopea generosa* collected from Puget Sound, Washington, as part of a long-term study of population genetics, maturation dynamics, and disease status.

RESULTS AND DISCUSSION

An important difference between the descriptions of *Mya abrupta* and *Panopea generosa* (see Introduction) is apparent. Contrary to Conrad (1849), Gould (1850, 1852) described his specimen as having an anterior gape, a difference evident in the respective holotypes (compare Figs. 1, 4). While compression during fossilization can lead to an apparent narrowing between the gape the valves along the

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FIGS. 1–3. *Panopea abrupta* (Conrad, 1849), holotype, USNM 3608 (scale bar = 5 cm). FIG. 1: Dorsal view showing the relatively narrow width of the gape of the valve along the anterodorsal margin; FIG. 2: Left lateral view; FIG. 3: Right lateral view. All images © Michael K. Brett-Surman, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution.

anterodorsal margin, compression would in turn accentuate the opposing posterior gape, which is not evident in Conrad's holotype.

The two species were synonymized without explanation by Gabb (1869: 89–90), who used the later name *generosa*. Dall (1898: 830–831) subsequently examined both holotypes, concluding that the two represent different species: *P. abrupta* “seems entirely distinct from the *P. generosa*, being a smaller, more slender, and more equilateral species.” Following concurrence by Arnold (1903: 182–183), Dall (1909: 133) reiterated the differences: “Conrad's type. A smaller, more equilateral, and more slender species than Gould's recent shell.”

Clark (1918: 161–162) described the differences between the Recent and fossil taxa in more detail, using the name *Panopea estrellana* (Conrad, 1857) for *P. abrupta* (Clark was not wholly convinced that the two fossil taxa, *P. abrupta* and *P. estrellana*, were the same):

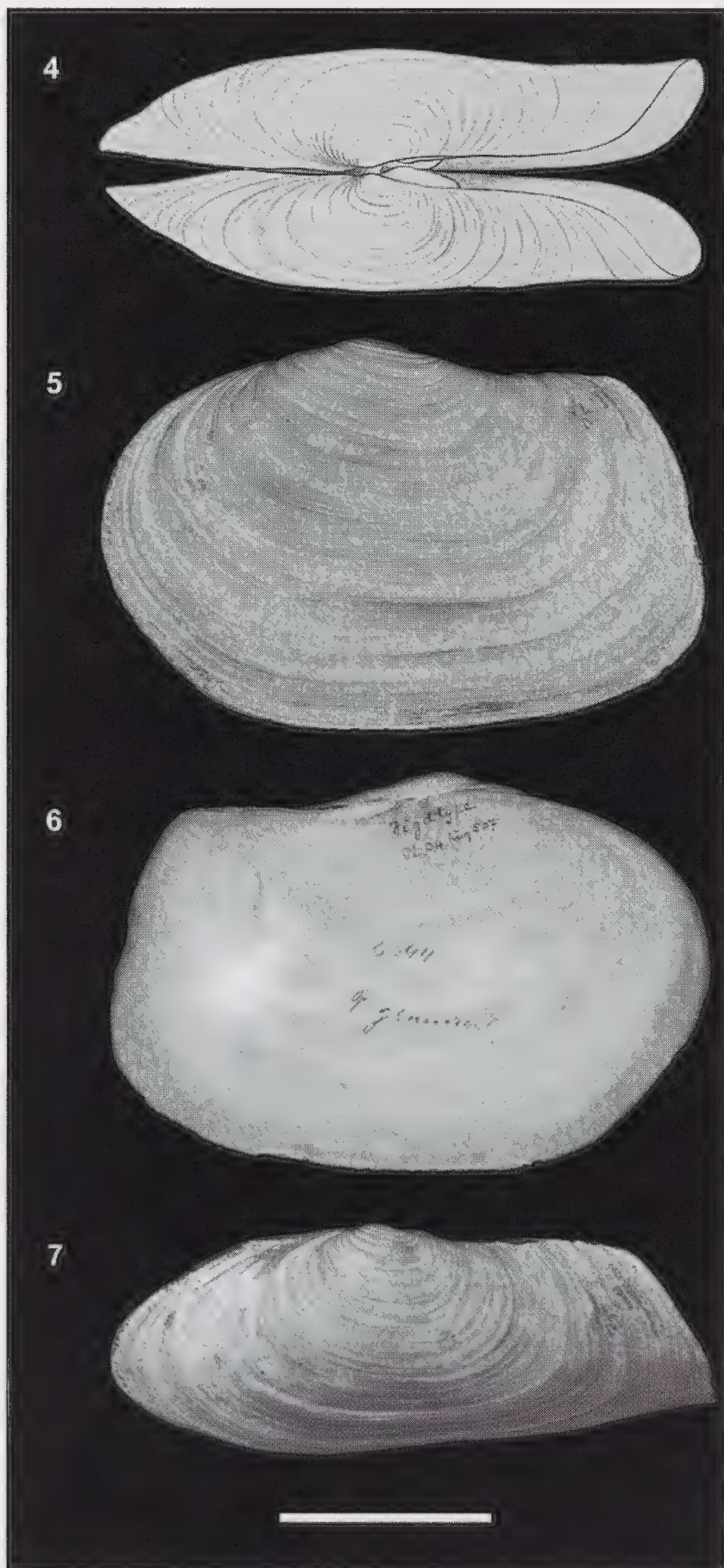
“The Recent species, *P. generosa* Gould, is rather variable in outline and sculpturing; this is also true of the form found in the Lower Miocene and Oligocene, referred to here as *P. estrellana*. Some authors have concluded that the variations of the Recent and Oligocene–Lower Miocene forms are so great that they can not be separated as distinct species. After examining a considerable number of specimens from the Lower Miocene and the Oligocene and of the Recent, the writer believes that the Oligocene–Lower Miocene form is distinct [...]. The most important differences between *P. cf. estrellana* and *P. generosa* appear to be that the former is somewhat longer in proportion to the height and has less conspicuous beaks. The posterior dorsal edge on *P. cf. estrellana* is straight, while on *P. generosa* it is usually concave; on *P. cf. estrellana* there is a wide shallow sinus, which extends from the beaks to the lower side of the truncate posterior end; this is usually absent on *P. generosa*, though appearing on some specimens.”

Clark (1918: 161) indicated further that *P. generosa* is the Recent species: “The writer exposed an imperfect hinge of the right valve of a specimen of *P. cf. estrellana* from the *Agasoma gravidum* beds, apparently enough to show that there are specific differences between it and *P. generosa*.”

Grant & Gale (1931: 424–425) synonymized *P. estrellana* (= *P. abrupta*) and *P. generosa*, stating that “Conrad's figure is not unlike some specimens that would unquestionably be identified as *generosa*.” (These authors used the name *generosa* because they mistakenly thought that the earlier named *abrupta* was a junior homonym of *Pholadomya abrupta* Conrad, 1832 and could not be used. However, the latter is a true *Pholadomya*.) Although Grant & Gale addressed the plasticity of length versus width, the anterior gape characteristics of the two holotypes were not mentioned. Weaver (1943: 262) concurred with this synonymy, but continued to use the name *P. generosa* presumably because of the alleged homonymy.

Moore (1964: 83–84) placed *P. abrupta* and *P. generosa* in synonymy, based in part on a misinterpretation of Dall (1898):

“Dall (1890–1903, p. 830–831, 1898) placed *Mya* [= *Panopea*] *abrupta* in synonymy with



FIGS. 4–7. *Panopea generosa* Gould, 1850, holotype, USNM 5894 (scale bar = 5 cm). FIG. 4: Dorsal view showing the relatively broad width of the gape of the valve along the anterodorsal margin (after Gould, 1860: pl. 34, fig. 507b); FIG. 5: Left lateral view; FIG. 6: Internal view. © Ellen Strong, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution); FIG. 7: Left dorsal view. © Jordan T. Watson, University of Washington.

Panopea generosa Gould because he thought that Deshayes was describing a new species, *Panopoea abrupta*, when actually Deshayes was simply changing the generic assignment of *Pholodaomya* [sic] *abrupta* to *Panopea*. Thus

the proper name for the *Panopea* originally described by Conrad (1849, p. 723) from the Astoria formation is *Panopea abrupta* (Conrad) and the name *P. generosa* should be placed in synonymy."

Finally, Yonge (1971: 26) discussed the biology of *Panopea* in detail, providing a review of the genus, referring throughout his paper to the Recent eastern Pacific species as *P. generosa*, and stating that "the valves are truncated ... and gape widely at both ends."

Our detailed comparison of both holotypes with extant material revealed a striking difference in morphology. The anterior gape, distinctly present in Gould's holotype (Fig. 4) and explicit in his description, but clearly absent in Conrad's fossil (Fig. 1), is also present in every contemporary specimen examined, from small juveniles to the largest adults ($n > 4,000$). While no significant differences in morphology were observed between Gould's holotype and all comparative material examined, Conrad's holotype differs significantly in the ratio of valve width to valve length (Fig. 8).

As mentioned above, a possible explanation for the dissimilarity in gape width is anterior compression during fossilization, which could presumably occlude the anterior gape in the holotype of *P. abrupta*. To investigate this idea, the valves of preserved Recent specimens of a wide range of size and age were compressed anteriorly, producing three clear results: first, the medial valve sections were no longer parallel; second, the region of maximal width occurred at the posterior margin instead of below the umbo; and third, the compressed specimens were no longer orthogyrate. These conditions are not evident in the holotype of *P. abrupta*: the valves are distinctly parallel, the maximal width is medial, and it is orthogyrate, with no prosodetic gape.

The ecologically important Recent species has been commercially harvested since 1969 (Goodwin & Pease, 1991) and farmed since 1996 in the northeastern Pacific (Straus et al., 2008), where it is reported to occur from Cedros Island, Baja California, Mexico (Ignacio Leyva Valencia, Centro de Investigaciones Biológicas dle Noroeste, Mexico, pers. comm., Sept. 4, 2009), to Kodiak Island, Alaska (Coan et al., 2000). A putative junior synonym, *Panopea japonica* A. Adams, 1850, occurs in the northwestern Pacific from Sakhalin Island, Russia to Kyushu, Japan (Coan et al., 2000). The Miocene fossil, *P. abrupta*, has been reported to occur in the coastal ranges of California, Oregon, and Washington (Weaver, 1943).

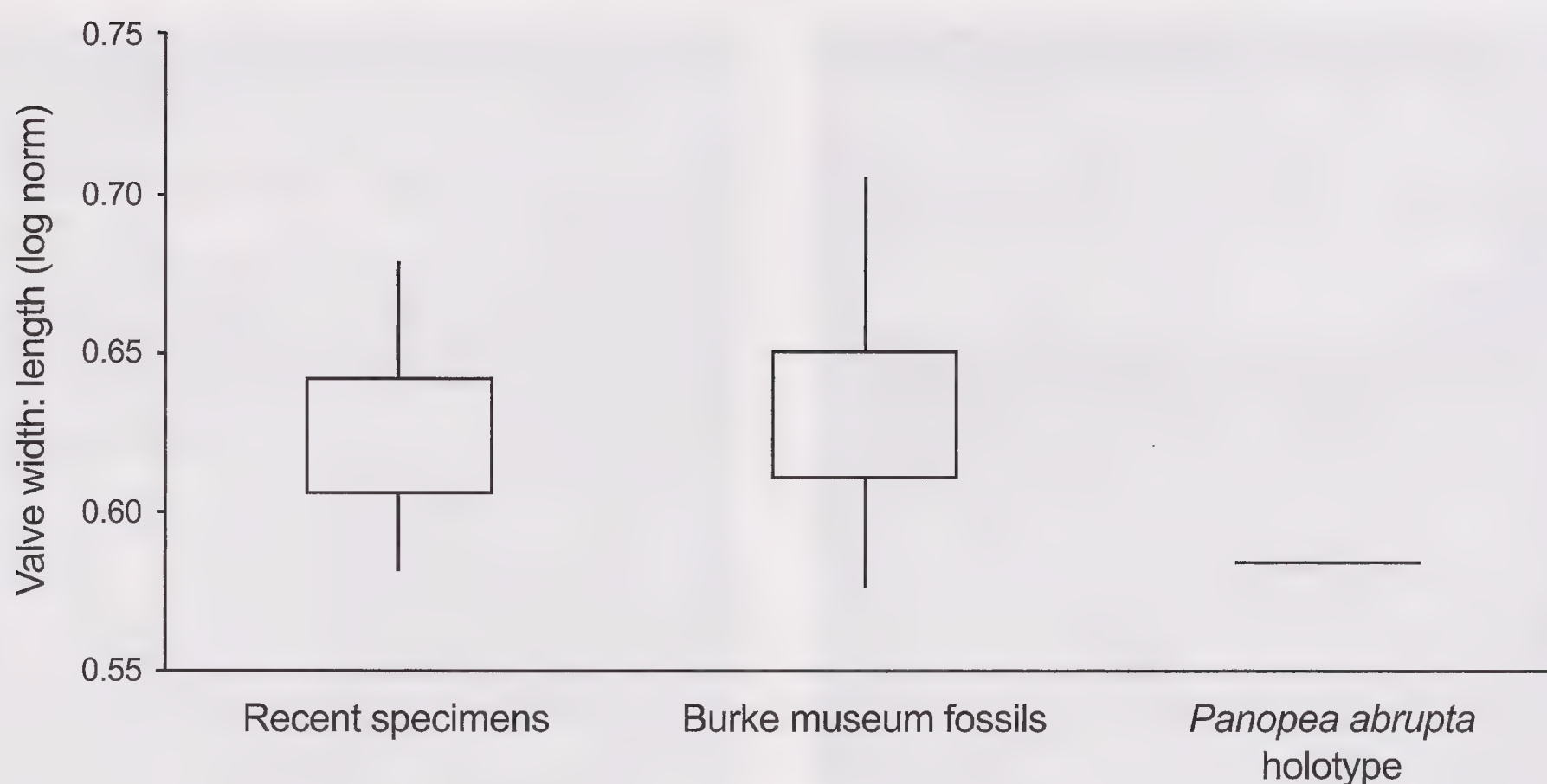


FIG. 8. Box-whisker plot of log-normalized ratios of valve width to valve length for recently collected specimens of *Panopea generosa* ($n = 41$), Oligocene and Miocene material of *Panopea* ($n = 30$), and the holotype of *Panopea abrupta* (USNM 3608).

Of 16 peer-reviewed publications mentioning the Recent species, resulting from a search of the malacological literature from 1969–1982, none used the name *P. abrupta*. But following Bernard's (1983: 59, 70, note 104) synonymization of the two species, based on Moore's (1964) erroneous paraphrasing of Dall (1898), an abrupt shift is evident. From that time to the present (1983 through May 2009), of 44 peer-reviewed publications, only three used the name *P. generosa* for the extant species (Breen & Shields, 1983; Boyer & Goddard, 1999; Boyer, 2001).

The earliest appearance in the peer-reviewed literature of the name *P. abrupta* in place of *P. generosa* was published by Sloan & Robinson (1983); Sloan & Robinson (1984) subsequently mention the synonymy citing Bernard (1983) as the authority. This error has been perpetuated in the scientific literature since 1984, but the differences are clear: *P. generosa*, unquestionably the proper name for the Pacific geoduck, is hereby formally resurrected from the synonymy of *P. abrupta*.

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REGENERATION OF THE INHALANT SIPHON OF *MESODESMA MACTROIDES* (DESHAYES, 1854) (MOLLUSCA: BIVALVIA)

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INTRODUCTION

Infaunal biota faces the compromise between predation avoidance and contact with the surface to maintain such biological functions as feeding, excretion, respiration, and reproduction. A compromise is attained, in the case of bivalves, through the siphons, optimising the interaction with the superficial environment (McLachlan et al., 1995). However, the exposure of these structures can enhance the risk for predation, making infaunal bivalves more vulnerable to tissue cropping by browsing feeders, such as crabs (Kamermans & Huitema, 1994), pelagic juvenile flatfishes (Trevallion et al., 1970) and birds (Zwarts, 1986). Siphon cropping has been reported for several bivalve species (Trevallion, 1971; Hodgson, 1982; Peterson & Quammen, 1982; Zwarts, 1986).

Many bivalve species have siphons, which can be seen as a renewable resource, if they regenerate after cropping (Penchaszadeh, 1983; Pekkarinen, 1984; Riera, 1995; Luzzatto & Penchaszadeh, 2001). Such processes function as secondary production to higher trophic levels in food webs. However, regeneration occurs at the expense of somatic growth and reproduction, affecting fitness (Geller, 1990; Peterson & Quammen, 1982; Kamermans & Huitema, 1994; Irlandi & Mehlich, 1996).

The yellow clam *Mesodesma mactroides* is an intertidal suspension-feeder, well adapted to its life mode (Narchi, 1981). It is an endemic infaunal inhabitant of the Atlantic coast of South America from southern Brazil to northern Patagonia, Argentina (Castellanos, 1970). In Argentina, its populations occur over 375 km of sandy beaches.

The inhalant siphon of *M. mactroides* is fringed with three series of unpigmented tentacles. The innermost series comprises eight tentacles, the largest and most ramified of the crown, which are directed inward as water enters the mantle cavity. These primary tentacles

are interspersed with by small foliose tentacles, which are also inwardly directed, so that the inhalant aperture is, in effect, covered by a coarse sieve when active (Narchi, 1981).

In this study, we conducted the regeneration process of artificially cropped inhalant siphon of *M. mactroides* at different seasons and levels of artificial severing to establish regeneration time in each condition.

MATERIALS AND METHODS

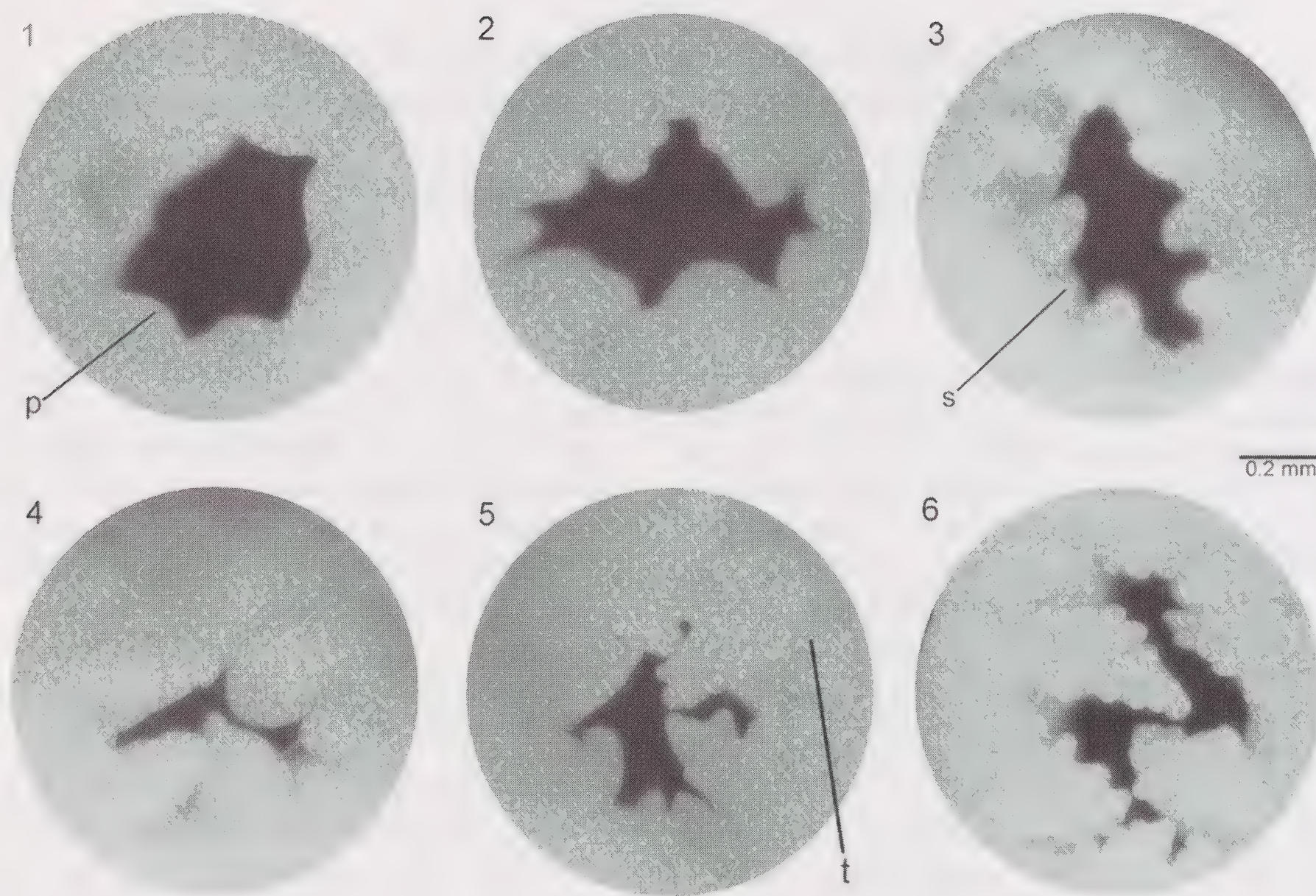
Individuals of *M. mactroides* were collected at Punta Mogotes beach, Argentina (37°59'S, 57°33'W). For a standardized size range, only clams with shell length 4–6 cm were used. They were placed in 96 cm³ plastic aquariums with sand in an open system of unfiltered seawater. Before starting the experiments the animals were maintained for acclimation under these conditions for two days. In order to maintain a stable photoperiod characteristic of each season, artificial illumination was controlled. Water temperature was measured with an alcohol thermometer to the nearest 1°C and salinity with a refractometer to the nearest 1 ppm. The averages winter and spring temperature were 10.5 (± 2.9)°C and 15.7 (± 3.4)°C respectively. All systems simulated reported field densities of 577 individuals/m² (Bastida et al., 1991). To make the siphon nipping, the inhalant siphons were cut using surgery scissors after being placed in low oxygen sea water and relaxed with a solution of MgCl₂, following the procedure of Miloslavich et al. (2004).

Morphology of regenerating tentacle crown was studied on fixed tips (4% seawater formaldehyde) of nipped siphons under a stereoscopic microscope. The regenerating crown of two randomly chosen individuals was photographed each two days, during a 20-day period and then at day 30. Pictures were classified according to the regeneration degree

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FIGS. 1–6. *Mesodesma mactroides*. Sequence of regeneration of the tentacle crown during spring. primary tentacles (p), secondary tentacles (s), tertiary tentacles (t). FIG. 1: One day; FIG. 2: Two days; FIG. 3: Four days; FIG. 4: Six days; FIG. 5: Eight days; FIG. 6: Twelve days.

of siphons, as described in previous studies on the genus *Donax* (Miloslavich et al., 2004; Luzzatto & Penchaszadeh, 2001).

The primary tentacles were used as a parameter of siphon regeneration, because they grow until full regeneration. In the following experiments, the lengths of the 5 primary tentacles of two individuals of each group were measured (ten tentacles in total) under stereomicroscope each two days until the tentacles stop growing. To avoid the tentacles retraction, each individual was relaxed and inhalant siphon was cut thereafter.

Effect of Siphon Nipping at Different Cut-Levels

To study the effect of the level of cut on time and regeneration pattern, 80 yellow clams were divided into two groups. The distal 1 cm of the inhalant siphon was cut in one group and the distal 5 cm in the other. The clams were returned to the tank.

Seasonal Regeneration Rate

In order to compare differences in regeneration rate between winter and spring, the distal 1 cm of the inhalant siphon was cut to one group of 40 individuals in each season.

Effect of Laboratory Conditions

A field experiment was conducted in a plastic tank of 96 cm³ during spring. It was burrowed into the beach until flush with the sand and covered with a plastic net of 1-cm mesh size to prevent the escape of clams. The distal 1 cm of the inhalant siphon was cut to one group of 40 individuals.

Data Analysis

Data were analysed with repeated measurements ANOVA (rmANOVA). The principal effects were adjusted for sphericity violation using the corrections of Greenhouse-Geisser (G-G), Huynh-Feldt (H-F) y lower bound estimate (Lowr. Bnd). The results were analysed *a posteriori* with the test of Tukey.

RESULTS

In the winter experiment, clams developed the first rudiments of siphons at the first day after treatment. On the sixth day, the secondary tentacles started developing. On the twelfth day the tertiary tentacles started developing. In

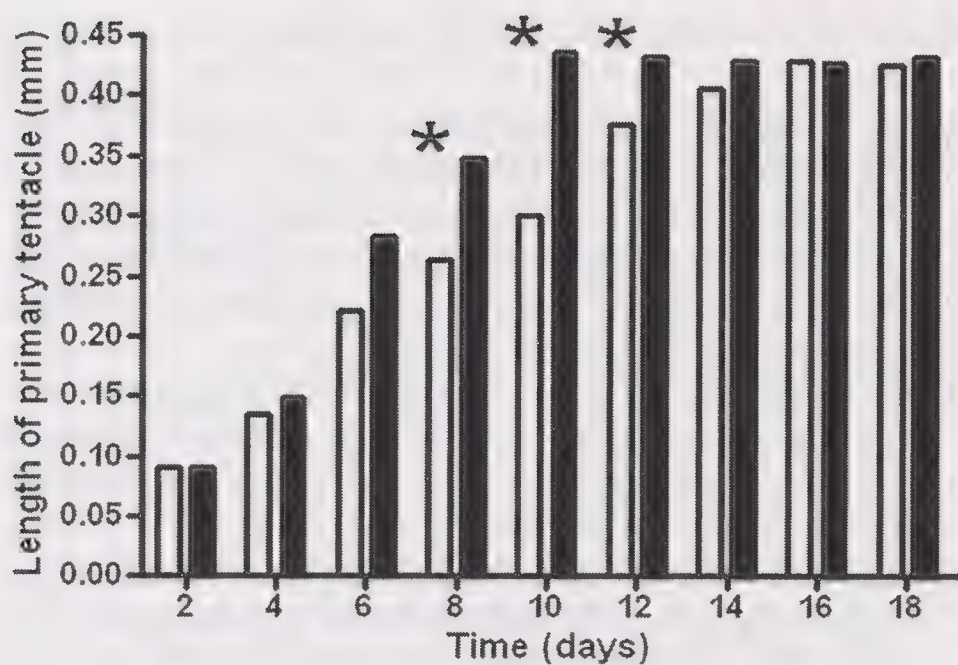


FIG. 7. Inhalant siphon of *Mesodesma mactroides*. Rate of regeneration of primary tentacles in different seasons. The black bars correspond to winter experiment and the white bars to spring experiment. Stars indicate statistical significant differences.

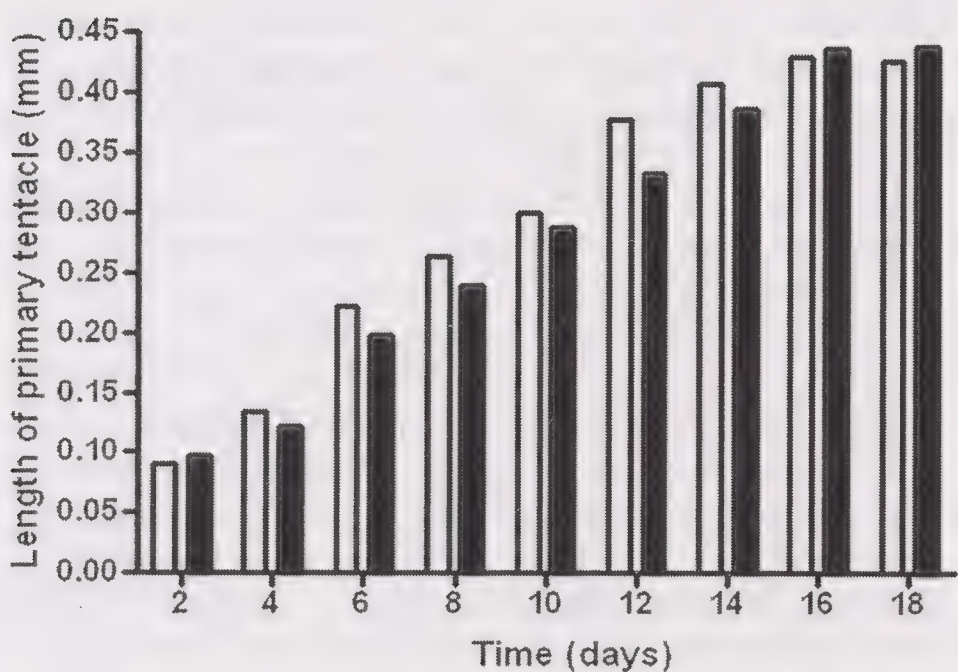


FIG. 8. Inhalant siphon of *Mesodesma mactroides*. Rate of regeneration of the primary tentacles in different levels. The black bars correspond to the individuals nipped at 5 cm and the white bars those nipped at 1 cm.

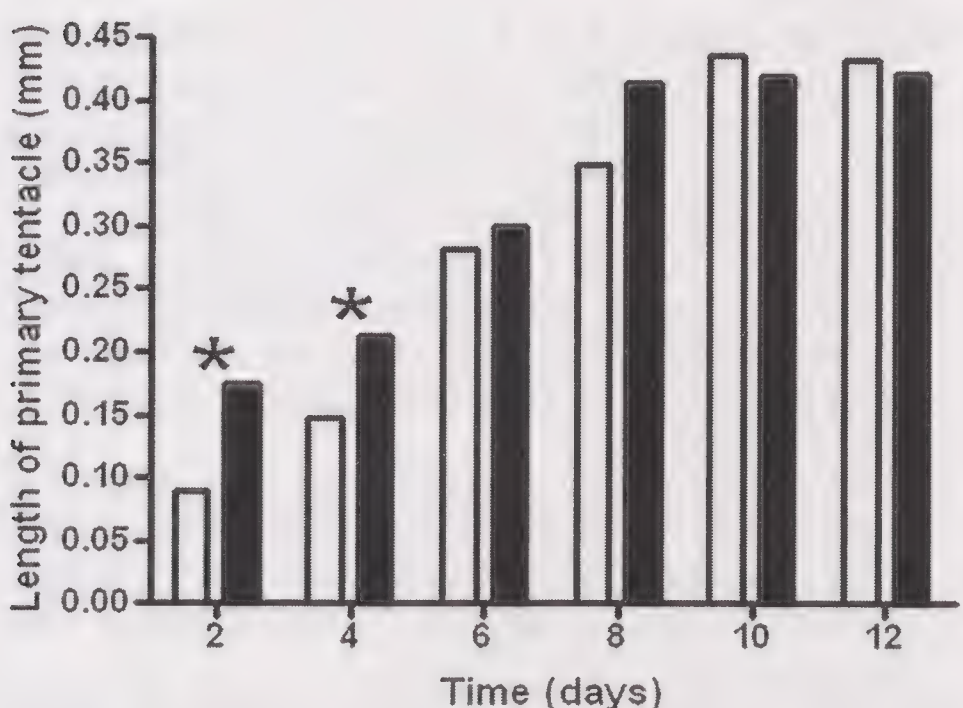


FIG. 9. Inhalant siphon of *Mesodesma mactroides*. Rate of regeneration of the primary tentacles in different experimental conditions. The black bars correspond to the laboratory experiment and the white bars to the field experiment. Stars indicate statistical significant differences.

spring, the regeneration took place faster than in winter. The first rudiment of siphon appear at the first day after treatment (Fig. 1), the secondary tentacles appeared six days after cutting (Fig. 3) (as in winter), but the tertiary tentacles eight days after that (Fig. 5). Figures 1 to 6 show the sequence of regenerations in spring.

Effect of Siphon Nipping at Different Cut-levels

No significant differences were found between treatments ($F = 1.67$; $df = 8$; $p > 0.05$).

Seasonal Regeneration Rate

Significant differences were found between winter and spring treatments ($F = 9.19$; $df = 5$; $p < 0.05$), and the test of Tukey showed different spread from the eight day until the end of the experiment.

Effect of Laboratory Conditions

Significant differences in tentacle length of spring field and laboratory treatments were found ($F = 7.66$; $df = 5$; $p < 0.05$). The test of Tukey also demonstrated significant differences as early as the fourth day, showing a faster growth in the laboratory experiment than in field experiment.

DISCUSSION

The regeneration process started a day after the ablation of the distal end of the inhalant siphon, when the primary tentacles initiate their development. The most dramatic events in the regenerating process of the inhalant siphon were detected within the first 96 hours after the treatment, with fast regeneration of primary and secondary tentacles, whereas the regeneration of tertiary tentacles delayed until the twelfth day in winter and eighth day in spring. Therefore, primary and secondary tentacles must play a more important role in providing basic functionality to the siphon. The slow process of regeneration observed within the first day after ablation of the tentacle crown occurs probably due to the malfunctioning of the siphon addition the physiological adequation needed for the tissue reparation, therefore limiting the food and oxygen intake of individuals with removed tips.

The regeneration time registered during both season experiments was longer than that reported by Luzzatto & Penchaszadeh (2001) for *Donax hanleyanus*, Miloslavich et al. (2004)

for *D. denticulatus*, and Pekkarinen (1984) for *Macoma balthica*.

The time in the regeneration process of the primary tentacles was related with the season (Fig. 7). Similar results were found in *Nuttallia olivacea* by Tomiyama & Kinuko (2006). This could be explained by the higher temperatures in spring, which accelerates the process or a higher food intake due to spring algal blooms. The rate of regeneration in *M. mactroides* was independent of level of siphon ablation (Fig. 8).

In the field experiment, the total time required to complete regeneration was similar to that under laboratory conditions, but in the former case, the process started sooner (Fig. 9). The rapid initial tentacular growth in field conditions suggests a reallocation of energy to crown formation. The delay in the regeneration start in the laboratory experiment probably was due to some non-simulated environmental variable, such as wave frequency.

This optimizes filtration, which would be of high energetic cost for the individuals of the field experiments due to the amount of suspended matter to filter.

Siphon loss reduces burrowing depth (Zwarts & Wanink, 1989; Zwarts et al., 1994; de Goeij et al., 2001; Meyer & Byers, 2005), increasing the risk of lethal predation by crabs or shorebirds, and decreasing feeding activity (Peterson & Skilleter, 1994; Skilleter & Peterson, 1994; Zwarts et al., 1994; de Goeij & Luttikhuisen, 1998). Rapid siphon regeneration is probably necessary for bivalves to attain sufficient reburial depth as soon as possible (de Goeij et al., 2001). In *M. mactroides*, siphon nipping reduces the deep of burrowing increasing the mortality by predation (Cledón et al. submitted), as reported in the bibliography in other bivalves (Haddon et al., 1987; Smith et al., 1999; Whitlow et al., 2003). So the clams would need to regenerate the tentacle crown to improve filtration optimising the available energy for recovering the normal deep of burrowing.

In this study was observed that individuals belonging to the same clam population increased the regeneration rate from winter to spring. It is still to be tested if these rate influences in the time that the clams remain exposed predators.

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ON THE NAMES OF SOME WESTERN ATLANTIC *LITHOPHAGA* SPECIES
(BIVALVIA: MYTILIDAE)

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Alcide d'Orbigny (1842–1853) introduced numerous molluscan species in Sagra's work on the natural history of Cuba. The exact publication dates of this important work have never been fully established. The date for the bivalve plates and associated captions had long been accepted as 1842, and d'Orbigny's names were deemed senior to those of such near-contemporary authors as Conrad (1846) and Philippi (1846, 1847).

However, Rosenberg (pers. comm., May 2006; 2009) has established that d'Orbigny's bivalve parts were published considerably later than 1842, perhaps as late as April 1853, and almost certainly no earlier than 1851. The date change of Sagra's work thus resulted in various priority issues involving numerous western Atlantic species. Mikkelsen & Bieler (2007) adopted an 1853 date and adjusted authorship and dates for 27 affected species occurring in the Florida Keys.

Three of d'Orbigny's (1853) well-established names of common western Atlantic *Lithophaga* species, *L. antillarum*, *L. bisulcata*, and *L. nigra*, were thus threatened by earlier names introduced by Philippi (1846, 1847). Their synonymy had long been accepted in the western Atlantic and mytilid literature (e.g., Abbott, 1974; Kleemann, 1983; Turner & Boss, 1962), but their priority had now become reversed. Following priority in this case could have resulted in the unfortunate situation that *Lithophaga antillarum* (d'Orbigny, 1853) would become *L. corrugata* (Philippi, 1846), whereas sympatric *L. nigra* (d'Orbigny, 1853) would be a junior synonym of the confusingly homonymous name *L. antillarum* (Philippi, 1847). The latter situation could possibly have been avoided by resurrecting *L. caribaea* (Philippi, 1847), which was published simultaneously with *L. antillarum*, but it still would replace commonly cited species names with ones that had fallen in disuse a very long time ago.

Mikkelsen & Bieler (2007: 413) invoked ICZN (1999) Article 23.9, Reversal of Precedence, to maintain prevailing usage of *Lithophaga antillarum* (d'Orbigny, 1853), introduced as *Lithodo-*

mus antillarum, over *Modiola corrugata* Philippi, 1846; of *Lithophaga bisulcata* (d'Orbigny, 1853), introduced as *Lithodomus bisulcatus*, over *Modiola appendiculata* Philippi, 1846; and of *Lithophaga nigra* (d'Orbigny, 1853), introduced as *Lithodomus niger*, over *Modiola antillarum* Philippi, 1847, *Modiola caribaea* Philippi, 1847, and *Lithophaga crenulata* Dunker, 1849. To satisfy Article 23.9.1.2, lists of works using d'Orbigny's names were provided and, after extensive literature searches, it was assumed that Article 23.9.1.1 also was met, which requires that the senior name had not been used as valid since 1899.

According to Article 23.9.2, d'Orbigny's three names – *Lithodomus antillarum*, *L. bisulcatus*, and *L. niger* – have been *nomina protecta* since the publication of Mikkelsen & Bieler (2007): "From the date of publication of that act the younger name has precedence over the older name. When cited, the younger but valid name may be qualified by the term *nomen protectum* and the invalid, but older, name by the term *nomen oblitum* ... In the case of subjective synonymy, whenever the names are not regarded as synonyms the older name may be used as valid."

In a recent discussion and illustration of *Lithophaga* type material, Kleemann (2009) reaffirmed the seniority of *Modiola appendiculata* Philippi, 1846, over *Lithodomus bisulcatus* d'Orbigny, 1853. During a subsequent exchange of messages, Dr. Kleemann kindly informed me of the existence of post-1899 usage of Philippi's names, particularly a work by Kühnelt (1930: 72 ff.), who had used *Modiola appendiculata*, *M. antillarum*, and *M. corrugata* as valid.

The discovery of post-1899 usage means that Article 23.9.1.2 was not met, a situation that the Code addresses in Article 23.10 (Erroneous Reversal of Precedence): "Prevailing usage must be maintained [Art. 82] until the Commission has made a ruling (i.e. an author discovering that such an erroneous action has occurred must not automatically use the older synonym or homonym)."

The case will have to be referred to the ICZN Commission for eventual ruling, but for now d'Orbigny's (1853) *Lithophaga* names (*L. antillarum*, *L. bisulcata*, *L. nigra*) are protected because of their prevailing usage.

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Karl Kleemann, University of Vienna, pointed out literature references to post-1899 usage of Philippi's *Modiola* names here discussed. Richard E. Petit, North Myrtle Beach, and two anonymous reviewers are thanked for comments on an earlier draft. Bivalve research is currently supported under U.S. National Science Foundation award DEB-0732854 to RB.

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THYLACODES – THYLACODUS – TULAXODUS:
WORM-SNAIL NAME CONFUSION AND THE STATUS OF *SERPULORBIS*
(GASTROPODA: VERMETIDAE)

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INTRODUCTION

In the worm-snail family Vermetidae, a large group of species (of still doubtful monophyly) is characterized by the absence of an operculum, the horny structure enabling other vermetids to fully or partially close the opening of the attached shell tube. Such species were traditionally described and grouped in the nominal genera *Serpulorbis*, *Lementina*, or *Thylacodes* (or variant forms of these names). Disputed authorships, numerous subsequent emendations, and conflicting type designations created a very complex situation, made worse by the introduction of similar sounding names such as *Thylacodus* and *Thylaeodus* for related, but not synonymous, taxa. With increasing involvement and mention of these vermetids in a wide range of biological studies, ranging from Recent and fossil diversity assessments to gene order research (e.g., Rawlings et al., 2001), taxonomic cleanup is urgently needed and the following note attempts to disentangle the confused situation.

TAXONOMY

The worm-snail genus *Tulaxodus* was formally introduced by Jean-Étienne Guettard (1770: 143 ff.) as “*Tulaxodus*, Tulaxode” with an extensive description of “caractere générique” as well as numerous vernacular references to recognizable published literature and illustrations. This work was usually cited by subsequent workers as dating from 1774, which is a slightly modified later edition with the same taxonomic content. Guettard’s (1770/1774) work should not be confused with his earlier publications describing worm-snails and other tube-building animals entirely in the vernacular (1766a, b; reprinted in 1777a, b). Keen (1961: 191) considered Guettard’s *Tulaxodus* unavail-

able because she viewed it as introduced in a non-binominal fashion in his 1774 publication. However, Guettard’s name is available as of his 1770 publication, for the same reasons given by Bieler (1992: 16, 17) when arguing for the validity of *Tenagodus* dating from the same work. The name satisfies the requirements of ICZN (1999) Articles 11(4) (1), 11(5), as well as 12(1), and other names introduced in the work are likewise in current use, such as *Kuphus*, *Uperotis*, and *Brechites*.

Blainville (1828: 40) introduced the name *Tulaxoda* with the statement “Tulaxode [using Guettard’s vernacular name]), Tulaxoda”, followed by a page reference to Guettard’s work (no year given) and a short description. *Tulaxoda* is not valid as a replacement name (because not citing the original name – ICZN [1999] Art. 33.2.1), but does qualify as a new description. No type species selection was found for it.

The name *Tulaxodus* was also subsequently modified to *Thylacodes*. The first to list it in this fashion appears to have been Agassiz (1846: 370, 381). His statement “Thylacodes – (V. Tulaxode Guett.)” was accepted as an emendation by Herrmannsen (1849: 575, 636), Newton (1891: 217), and Neave (1939–1940: 484). However, Agassiz only referred to Guettard’s vernacular name and his “*Thylacodes*” was dismissed as a *nomen nudum* by Keen (1961: 191), an action here followed.

Herrmannsen (1849: 575, 636) accepted Agassiz’s spelling of *Thylacodes* for Guettard’s name, which he misspelled *Tulaxodes*, and cited a prior reference to Guettard’s vernacular name “Tulaxode” (Deshayes, 1832: 1083) as well as Blainville’s (1828) *Tulaxoda*. Herrmannsen’s action is here accepted as a formal emendation of *Tulaxodus* to *Thylacodes*; his misspelling of Guettard’s original name cannot be confused with any other name then in existence, especially since he provided an

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exact page reference to Guettard's original *Tulaxodus* in this context. The emendation from (now correctly spelled) *Tulaxodus* to *Thylacodes* was reiterated by Newton (1891: 217), who credited Agassiz (1846) and Mörch (1862, see following discussion). *Tulaxodes* was subsequently mentioned by various authors, for instance as "Tulaxodes, Guett." in synonymy of *Vermetus* by H. Adams & A. Adams (1854: 357), as "Tulaxodes, Guettard ... 1774" in synonymy of *Thylacodes* "Guettard" by Mörch (1862: 65), and even as possibly related to belemnites, by Fleming (1837: 98). Paetel (1875: 218) synonymized *Tulaxoda* Blainville under "Tulaxodes Guett.", while considering the latter as the "current and correct" name for the group (1875: iv; here translated from the original German). Somewhere along the line *Tulaxodes* was probably intended as an emendation of *Tulaxodus* Guettard, but was not found formally introduced as such and is here treated as an incorrect subsequent spelling. Sacco (1896: 10) also addressed "*Tulaxodes* Guett. 1774" and stated he would have accepted its priority if the name had not been ill composed ("mal composto"). He accepted Agassiz's 1846 action as an emendation to *Thylacodes*, but considered that name junior to *Lemintina* Risso, 1826.

Lemintina Risso, 1826 (p. 114, also as *Lementina* in caption to pl. 2 on p. 432) was based, by monotypy, on *Lemintina cuvieri* Risso, 1826. Both spellings were subsequently used. The earliest (first reviser) choice was made by Herrmannsen (1849: 580, 581) who listed both names and used *Lemintina* instead of *Lementina*, but other authors continued employing *Lementina*, including Paetel (1875: 107, iv) who listed that spelling as "current and correct" (here translated from the original German). The identity of *L. cuvieri* remained a matter of discussion, with most authors interpreting the original figure as representing the large non-operculate vermetid of the Mediterranean. That species has been referred to by many names, including *Serpulorbis polyphragma* Sasso, 1827, and *Vermetus gigas* Bivona Bernardi, 1832. Many authors (e.g., Keen, 1961: 202) accepted *Serpula arenaria* Linnaeus, 1758, as the senior name for this species (a choice in conflict with parallel usage in teredinid bivalves – e.g., Zammit Maempel, 1993 – and a topic beyond the scope of this paper). H. Adams & A. Adams (1854: 359), for instance, placed *Lementina* with "?" in the synonymy of *Serpulorbis*, and stated "The genus *Lementina* of Risso is most probably

a badly-observed and incorrectly-figured *S. arenaria*, an inhabitant of the Mediterranean." The stylized original figure of a living specimen (Risso 1826: fig. 16) appears to blend features of Vermetidae and serpulid polychaetes. Chavan (1944: 338) stated that the "coquille-type est une tube d'Annélide," and the remaining tube fragments in the Risso collection (MHNH Paris) labeled *L. cuvieri* were recognized as polychaete tubes by Arnaud (1978: 114). In any case, even if interpreted as a vermetid species, *Lemintina* would be a junior subjective synonym of *Thylacodes*, as explained below. *Limentina* is a misspelling also appearing in the literature (e.g., Suter, 1913: 259).

Mörch's (1862: 64 ff.) monographic revision of the group adopted Guettard's taxon as "*Thylacodes*, Guettard, 1774" – the form emended by "Agassiz" [i.e., Herrmannsen, 1849, see above] and used it as senior synonym of a group of several nominal genera, including *Serpulorbis* Sasso, 1827. *Serpulorbis* had been introduced by Sasso (1827: 483) with the type species, by monotypy, *Serpulorbis polyphragma* Sasso, 1827. The synonymy of Guettard's and Sasso's genera was widely accepted, an example being Newton (1891: 217), who treated *Serpulorbis* Sasso, 1827 in synonymy of *Thylacodes* "Guettard, 1770." As will be shown below, *Thylacodes* and *Serpulorbis* are objective synonyms sharing the same type species.

Keen (1961: 191), who viewed Agassiz's (1846) usage of the name *Thylacodes* as a *nomen nudum*, apparently did not consider Herrmannsen (1849), and accepted Mörch (1862: 64) as the first author who validly introduced this taxon (Mörch had credited *Thylacodes* to Guettard, but repeated Herrmannsen's mistake of listing the original name as "*Tulaxodes*," not *Tulaxodus*). Guettard's (1770) work introducing the genus did not associate nominal species (other than in the vernacular). Mörch (1862) included 21 nominal species in *Thylacodes*, but like all authors before him did not indicate a type species. Keen recognized the synonymy of *Thylacodes* "Mörch, 1862" with *Serpulorbis* Sasso, 1827, and she selected a type species that would make them objective synonyms: "*Serpulorbis polyphragma* Sassi, 1827 = *Serpula arenaria* Linné, 1758." As objective synonyms since 1961, *Serpulorbis* and *Thylacodes* can no longer be employed in a genus-subgenus relationship, as was done previously, for instance by Vaillant (1871).

Because Herrmannsen's (= Mörch's, = Newton's) *Thylacodes* is an emended form of

Tulaxodus, Keen's type species selection for *Thylacodes* also extends to the original *Tulaxodus*. Keen attempted to eliminate a junior synonym of *Serpulorbis* by assigning it the same type species by subsequent designation. This action, however, made *Thylacodes* the senior objective synonym.

In today's treatment (ICZN 1999 Art. 19.1), *Thylacodes* Herrmannsen, 1849, having been an unjustified emendation, would take its own author and date, and become a junior objective synonym of the original name, *Tulaxodus* Guettard, 1770. However, subsequent authors followed Agassiz, Herrmannsen, and Mörch, and the unjustified emendation *Thylacodes* became the form in prevailing use (prevailing usage is defined [p. 121 of the 1999 Code] as "usage ...adopted by at least a substantial majority of the most recent authors concerned with the relevant taxon, irrespective of how long ago their work was published"). ICZN (1999 Art. 33.2.3.1.) states "when an unjustified emendation is in prevailing usage and is attributed to the original author and date it is deemed to be a justified emendation." Until Keen's (1961) mistaken declaration of *Tulaxodus* Guettard as a *nomen nudum*, the majority of authors used the form *Thylacodes* and attributed it to Guettard. *Thylacodes* is here accepted as a justified emendation of *Tulaxodus* (i.e., Art. 33.2.3.1 does apply) and dates from Guettard, 1770. Thus, *Thylacodes* Guettard, 1770, has priority over *Lementina*/*Lemintina* Risso, 1826 (if interpreted as a vermetid gastropod) and over *Serpulorbis* Sasso, 1827.

Although *Serpulorbis* Sasso, 1827, is the more commonly used name in the recent literature, "reversal of precedence" cannot be applied under ICZN (1999) Art. 23.9, because *Thylacodes* has been used as a valid name after 1899 (e.g., in the descriptions of *Thylacodes caperatus* Tate & May, 1900, and *Vermetus (Thylacodes) capensis* Thiele, 1925).

In addition, *Tulaxoves* appears in the literature (listed by Scudder 1882: I-346, II-330, who refers to Guettard "1 86" [sic]). It is here considered an incorrect subsequent spelling.

The nominal genus *Tulaxodus* and particularly its emendation *Thylacodes* should not be confused with the unfortunately very similar *Thylaeodus* and *Thylacodus*, both introduced by Mörch (1860a: 48 and 1860b: 77, respectively), and also genus-group names within this family. *Thylaeodus* (Mörch, 1860a: 48) was introduced for vermetids without columellar folds or lamellae discussed earlier in that paper ["pour les Vermets sans plis," as opposed to

genus *Petaloconchus*, which has columellar shell lamellae]. Keen (1961: 191) selected as type species, by subsequent designation, *Bivonia contorta* Carpenter, 1857. To simplify matters, Keen (1961: 191) attempted making *Thylacodus* Mörch, 1860, a junior objective synonym of *Thylaeodus* by selecting the same type species, *Bivonia contorta* Carpenter, 1857, by subsequent designation. Keen referred to page 77 of Mörch's work, and stated he had originally included *Vermetus contortus* (Carpenter), *V. subcancellatus* Bivona Bernardi, *V. conicus* Dillwyn, and *V. contortus* var. *indentatus* Carpenter. However, *V. conicus* had not been included at all by Mörch, and *V. contortus* was indicated by a tentative "?". More importantly, on the following page Mörch (1860b: 78) clearly presented an original designation, here translated from the German original as "I therefore propose a subgenus *Thylacodus* for *Bivonia subcancellata* Biv., characterized by ...". ICZN (1999) Art. 68.2 applies, and Keen's subsequent designation of a type species for *Thylacodus* Mörch is invalid.

The following is a summary of the genus-group names discussed in this article:

Lementina Risso, 1826 [a variant original spelling of *Lemintina*].

Lemintina Risso, 1826 [available name, selected over *Lementina* by first reviser action of Herrmannsen (1849); a junior subjective synonym of *Thylacodes*, if interpreted as a vermetid mollusk].

Type species: *Lemintina cuvieri* Risso, 1826.

Limentina [incorrect subsequent spelling of *Lemintina*].

Serpulorbis Sasso, 1827 [available name; a junior objective synonym of *Thylacodes*].

Type species: *Serpulorbis polyphragma* Sasso, 1827.

Thylacodes Guettard 1770 [available name; a justified emendation of *Tulaxodus* Guettard, 1770].

Type species: *Serpulorbis polyphragma* Sasso, 1827.

Thylacodus Mörch, 1860 [available name; a vermetid, but not congeneric with *Thylacodes*].

Type species: *Vermetus subcancellatus* Bivona Bernardi, 1832.

Thylaeodus Mörch, 1860 [available name; a vermetid, but not congeneric with *Thylacodes*].

Type species: *Bivonia contorta* Carpenter, 1857.

Tulaxoda Blainville, 1828 [available name; a junior synonym of *Thylacodes*].

Without designated type species.

Tulaxodes [incorrect subsequent spelling of *Tulaxodus*].

Tulaxodus Guettard, 1770 [available name, emended by justified emendation to *Thylacodes*].

Type species: *Serpulorbis polyphragma* Sasso, 1827, Vermetidae.

Tulaxoves [incorrect subsequent spelling of *Tulaxodus*].

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LETTER TO THE EDITOR

COMMENTS ON THE VALUE OF COI FOR FAMILY-LEVEL FRESHWATER MUSSEL SYSTEMATICS: A REPLY TO HOEH, BOGAN, HEARD & CHAPMAN

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INTRODUCTION

Hoeh, Bogan, Heard & Chapman (2009; hereafter HBHC) raise a number of important criticisms of our recent analysis of family-level relationships among the lineages of the Palaeoheterodonta, Graf & Cummings (2006; hereafter G&C). We are pleased to have our conclusions scrutinized from other perspectives. HBHC also raise a number of questions about issues that we apparently did not explain in sufficient detail, and they report that the results of their reanalyses challenge our conclusions. We welcome their reanalysis and discussion. The objective of this article is to keep that debate alive by replying to HBHC.

HBHC discuss at least five points of disagreement with our methods of analysis or conclusions:

- (1) We did not include (or adequately justify exclusion of) COI sequences from the non-palaeoheterodont outgroup taxa (i.e., *Mytilus* and *Astarte*);
- (2) We did not include (or adequately justify exclusion of) COI sequences from three ingroup taxa (i.e., *Pseudomulleria*, *Coelatura*, and *Obliquaria*);
- (3) We did not transform our COI matrix to account for saturation;
- (4) We reached an erroneous conclusion about the monophyly of the Etheriidae; and
- (5) We reached an erroneous conclusion about the position of the Hyriidae.

These, of course, are all points open for debate, and we are grateful to HBHC for initiating this opportunity to consider them further. Their discussion of our methods and conclusions articulates well the differences in perspective we have regarding the ultimate purpose of performing phylogenetic analyses. We will take up each of these five points in order.

WE DID NOT INCLUDE COI FOR THE OUTGROUP TAXA

HBHC noted that we did not include COI sequences for either *Mytilus* or *Astarte* (the two non-palaeoheterodont outgroup taxa). As we explained in G&C, we excluded those sequences because they compromised the basal branches of our family-level phylogeny. This is evident in the reanalysis of the untransformed G&C matrix performed by HBHC (their fig. 5), as compared to G&C: fig. 2 (lower left: Combined Evidence, Problematic Included).

They correctly point out that if we had transformed our COI data, those effects on the basal branches of the phylogeny would have been minimized. Our general discussion of data transformation follows below. Our conclusion after preliminary analyses was that such divergent outgroup COI sequences contributed only confusion to the dataset and that their inclusion was unnecessary. With the exception of Graf & Ó Foighil (2000), previous analyses of the COI data applied in the G&C matrix did not include any non-palaeoheterodont sequences (Bogan & Hoeh, 2000; Hoeh et al., 2001, 2002; Roe & Hoeh, 2003). Rather, it had been assumed that the Palaeoheterodonta was monophyletic, and only *Neotrigonia* was necessary to root the unionoid tree. This is a reasonable assumption, given how well supported palaeoheterodont monophyly has been in previous studies of bivalve relationships (Hoeh et al., 1998; Giribet & Wheeler, 2002). We, however, wanted to include representatives from the pteriomorph and heterodont lineages in order to (at least nominally) test our hypotheses of the morphological synapomorphies diagnosing the higher-level taxa of the Palaeoheterodonta – something that had not been done before in the context of an analysis with representatives of all seven families of the subclass.

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As evidenced by every published COI analysis of freshwater mussel family-level phylogeny, this particular mtDNA fragment, while providing acceptable resolution within families, provides poor support for interfamilial relationships. Therefore, phylogenies derived solely from COI provide inadequate tests of hypotheses of freshwater mussel relationships at that level. Despite the fact that COI was a poor choice of characters for resolving those interfamilial relationships, it was the only molecular data available to a large sector of the tree (e.g., lasidium-bearing mussels) and had been used extensively in recent publications to make inferences about family-level relationships (Bogan & Hoeh, 2000; Graf & Ó Foighil, 2000; Hoeh et al., 2001, 2002; Roe & Hoeh, 2003). To meet the objectives of the G&C article to review and reanalyze the available data supporting the family-level phylogeny of the Unionoida, we had no choice but to rely on COI.

The problem with our untransformed COI matrix is that, even without *Mytilus* and *Astarte*, the data were full of noise – to the point that the majority of transformations traced to terminal branches (overall 56.9%, 1st position 56.9%, 2nd 62.0%, 3rd 56.8%; G&C: table 4). That is, most of the data were at best uninformative under parsimony, and given the amount of homoplasy observed (COI partition CI = 0.248; G&C: table 4), a large proportion were misinformative. We fail to see how this problem could be improved by adding two more long terminal branches to the analysis.

Transforming our matrix by excluding transitions occurring in the third codon positions would indeed have reduced the effects of saturation on the deeper nodes, but it would have also removed from the dataset many of the characters supporting shallower nodes (Swofford et al., 1996). Instead, we opted to limit the effects of COI to where it could do the most good or where it was the only sequence data available: the ingroup. In addition, we combined this faster-evolving mitochondrial gene with a 473 aligned-nucleotide fragment of the more-conserved nuclear locus 28S (where the data were available) as well as 59 morphological characters.

The fact that including *Mytilus* and *Astarte* COI sequences changes the ingroup topology is not an affirmation of the suitability of these data to the problem. Rather, it is indicative of the conflict within the dataset. G&C and HBHC each provided different methods for dealing with the problem of noise in the COI

dataset (both involving discarding portions of the available data because they were deemed inappropriate), but neither solved it – again, as evidenced by the weak interfamilial support in all analyses relying upon COI.

In summary, we did not include COI for the two outgroup species because doing so would have contributed only more noise to an already muddled dataset and because we had confidence in previous analyses of palaeoheterodont monophyly (Hoeh et al., 1998; Giribet & Wheeler, 2002).

WE DID NOT INCLUDE THREE PROBLEMATIC INGROUP COI SEQUENCES

HBHC are absolutely correct to be skeptical of a phylogenetic study that eliminates available data without justification. But, as we stated in G&C (p. 349), we excluded COI sequences for three taxa because of their “... inconsistency (relative to other available data) and their importance to family-level hypotheses of monophyly.” In the G&C paper, we ran all analyses both with and without the problematic taxa, provided a verbal description of the results on p. 353, and provided consensus cladograms (G&C: fig. 2). Moreover, on p. 374 we gave the following discussion:

“What makes these two sequences [*Pseudomulleria dalyi* and *Coelatura aegyptiaca*] problematic is not their conflict with the traditional classification. Rather, it is their inconsistent behaviour. In our COI Only analysis (not shown), these two sequences were placed in the strict consensus in a polytomy at the base of a (Unionidae + Margaritiferidae) clade that had no bootstrap support; Bogan & Hoeh (2000: fig. 1) resolved *Pseudomulleria* and *Coelatura* as the basal members of this clade. With the addition of 28S and morphology, *Pseudomulleria* migrated to a nonsensical position sister to the (*Unio* + *Cafferia*) clade, and *Coelatura* fell to near the base of the Palaeoheterodonta – and in at least a small number of MP trees, it was even placed outside of that clade (Fig. 2). When these two problematic sequences were excluded from the [Combined Evidence] analysis, *Coelatura* and *Pseudomulleria* were recovered in their traditional families, the Unionidae and Etheriidae, respectively (Figs. 2, 3). Scientifically, we are in no position to say that any of these various results is ‘incorrect’. However, it is our opinion that the available evidence does not warrant these two DNA se-

quences rejecting the null hypotheses that the Etheriidae and Unionidae are monophyletic.”

Obliquaria was discussed on p. 375. None of the concerns that we raised are addressed by HBHC. They simply reiterate their previous conviction that these inconsistently behaving sequences require no additional scrutiny.

Thus, we relied upon a dataset (and resultant phylogeny) that did not depend upon those problematic COI sequences because we had little confidence in the accuracy of the results those sequences provided in our analyses. The specific problem of *Pseudomulleria* is discussed below.

WE DID NOT TRANSFORM THE COI MATRIX

Regardless of whether or not HBHC refer to their parsimony analyses as unweighted, they are weighted since their process of matrix “transformation” is equivalent to an *a priori* weighting scheme. The matrix transformation to which HBHC refer has not, to our knowledge, been explicitly explained in previous papers, but we assume it refers to what Swofford et al. (1996) called “transversion parsimony.” For all third codon positions in the COI alignment, nucleotides are recoded as simply purines (G, A) or pyrimidines (C, T). This has the same effect as assuming a step-matrix wherein third position transitions are down-weighted to zero in the analysis of an untransformed matrix. When HBHC use the term “equal weighting,” they are strictly referring to how PAUP is treating their matrix: all character state changes in their “transformed” and “untransformed” matrices contribute equally to the final tree scores. However, by performing the transformation, HBHC have implicitly built their step-matrix into their character set rather than implementing a separate assumption set.

HBHC object to our not down-weighting the third position transitions of the G&C matrix in order to correct for the well-known problem of saturation in COI. In our analyses, we considered it sufficient to combine those COI data with a more conservative nuclear gene fragment (473 aligned positions of 28S) as well as 59 morphological characters. Thus, we added both more characters and more taxa to the troubled COI dataset, as has long been prescribed as a solution for dealing with long-branch issues and for minimizing the potentially misleading biases of individual data partitions (Graybeal, 1998; Hillis, 1998; Naylor & Brown, 1998).

MONOPHYLY OF THE ETHERIIDAE

As discussed by HBHC on p. 314, they disagree with our treatment of the Etheriidae as monophyletic. The G&C preferred dataset, which “... contained a *Pseudomulleria* terminal but only included morphological and life history characters in the matrix, confirmed the monophyly of the Etheriidae. Alternatively, Bogan & Hoeh’s (2000) analysis of COI DNA sequences, which included data for *Etheria*, *Acostaea*, and *Pseudomulleria*, indicates that *Pseudomulleria* is a unionid, as does Woodward’s (1898) anatomical study, thus rejecting the concept of a monophyletic Etheriidae.” Two aspects of HBHC’s argument require comment.

First, *Pseudomulleria* does not resemble a unionid in either its conchology or soft-anatomy. While it is true that Woodward (1898) used the word “Unionidae” to classify the two specimens of *Pseudomulleria dalyi* that he described and figured, he applied that term as an indication that this species was a freshwater mussel and not an oyster – that the anatomy was more similar to *Unio* and *Anodonta* than to other “... such monomyarian forms as *Meleagrina*, *Ostrea*, *Anomia*, and *Pecten*...” (p. 90). Further, Woodward considered both *P. dalyi* and *Acostaea rivoli* (= *lobata*) to belong to the same genus (*Mulleria*), indicating his assessment that those species are closely related. Nomenclatural argumentation aside, Woodward provided the following description of the mantle of *Pseudomulleria*:

“The mantle folds are almost completely separated from one another, being united at two points only, viz., at the posterior attachment of the gills, thus separating an inhalent from an exhalent orifice, and dorsally from the posterior end of the hinge-line for about one-quarter of the distance between this point and the attachment of the gills” (p. 87).

Whereas this description does not match what is known for any species of the Unionidae (e.g., there is no supra-anal aperture), the fusion of the mantle between the incurrent and excurrent apertures matches the condition otherwise known from only the Mycetopodidae and the Etheriidae. Most authorities of the 20th century that have studied the genera in question have noticed the striking conchological and soft-anatomical similarity between *Acostaea* (from South America) and *Pseudomulleria* (from India). Historical “Just-So” stories of convergent evolution in the characters of these lineages were invoked not because anyone thought

that the two monotypic genera were actually morphologically dissimilar but to explain their geographical disjunction in a paradigm lacking continental drift. This was commented upon by Yonge (1978: 440):

“Without realizing the effectively identical structure of the animals of *Acostaea* and *Pseudomulleria* or their unique manner of growth into the monomyarian adult, these two genera have been thought of as arising independently as a result of convergent evolution. ... But the changes both have undergone are so unique – so totally unlike those undergone by any other monomyarians – that it is excessively difficult to maintain that these could have arisen independently in two far distant river systems.”

That other freshwater mussels like *Modellnaia* (Heard & Hanning, 1978) and perhaps *Bartlettia* (Parodiz & Bonetto, 1963) arrived at somewhat etheriid-like conchologies through convergence does not automatically make asymmetrical shells resulting from a cementing lifestyle homoplastic in every case.

Secondly, HBHC, Bogan & Hoeh (2000), and subsequent works deriving conclusions from this hypothesized etheriid polyphyly (Bogan, 2007; Bogan & Roe, 2008) have given this single sequence of one gene fragment from one specimen a lot of weight. It has yet to be made explicit why this particular, oddly behaving (see above) sequence should be considered representative of *Pseudomulleria dalyi*. But more importantly, HBHC provide no evidence that they appreciate how incongruous what is known of the soft-anatomy of *Pseudomulleria* is with its placement among the unionids, and no specimen voucher or figure has ever been indicated. In the 10 years since the hypothesis was proposed, no additional data has been presented in support of etheriid polyphyly, and the rest of the data gathered over the past 110 years (meager as it is) stands against it.

In our study, we took a conservative approach and recognized that this single ambiguous data point was not sufficient to reject the traditional hypothesis of etheriid monophyly. Thus, we regarded this sequence as “problematic” and did not include it in our preferred matrix. (The same logic applies to the published COI sequences for *Coelatura* and *Obliquaria*, which we also deemed problematic and that bear upon the monophyly of the Unionidae and Lampsilini, respectively.)

RESOLUTION OF THE POSITION OF THE HYRIIDAE

Based upon the HBHC reanalyses of our G&C matrix, they find that only the unweighted parsimony analysis (their fig. 5) recovers a clade composed of (Hyriidae + Etheriidae + Iridinidae + Mycetopodidae), the same result reported from previous analyses emphasizing morphological characters. However, they prefer the results recovered by both Bayesian Inference (fig. 3) and MP analysis of their transformed matrix (fig. 4). The contentious position of the Hyriidae has been a persistent issue since the first phylogenetic analyses of freshwater mussels: morphology supports one result, COI another. Previous hypotheses of the phylogenetic position of the Hyriidae were discussed by G&C.

We reexamined for ourselves the COI portion of the G&C matrix (i.e., we excluded all taxa that had no COI sequences and all non-COI characters) under parsimony to evaluate further the power of COI to discriminate alternative topologies. All analyses were performed with the portable version of PAUP*4b10 (Swofford, 2002). Beginning with unweighted analyses, we performed three separate heuristic searches (“hsearch addseq=random nreps=100”): (1) unconstrained, (2) constraints enforced to recover only trees with a monophyletic Hyriidae basal to the rest of the species in the order (nicknamed “Hyriidae Basal”), and (3) constraints enforced to recover only trees with a clade composed of the species of the Hyriidae, Etheriidae, Mycetopodidae, and Iridinidae (nicknamed “Hyriidae + Etherioidea”). In the latter constraint tree, the *Pseudomulleria* sequence was allowed to fall among the (Unionidae + Margaritiferidae) species. Each of the constrained topologies was compared to a single unconstrained tree using both the Templeton and Winning-Sites tests (Felsenstein, 2003) (both implemented in PAUP*; “pscores /nonparamtest=yes”). We also performed the same tree searches assuming a step-matrix wherein third position transitions were down-weighted to zero (i.e., transformed). The results of these analyses are presented here in Table 1.

The Templeton and Winning-Sites tests are paired-sites tests that compare alternative topologies statistically, with p values indicating if one tree is significantly better than another, given the amount of conflict in the dataset (Felsenstein, 2003). Thus, a $p < 0.05$ indicates

TABLE 1. Results of nonparametric tests comparing unconstrained and constrained topologies using both unweighted and transformed COI data from G&C. A single tree unconstrained topology (“best”) was compared to the topologies recovered from searches with constraints enforced. Constraint “Hyriidae basal” = (Neotrigonia, (Hyriidae, (all other species))); constraint “Hyriidae + Etherioidea” = (Neotrigonia, (Hyriidae + Etherioidea), (all other species)). P-scores of Templeton and Winning-Sites nonparametric tests (Felsenstein, 2003) comparing each constraint topology with the “best” tree are given parenthetically. *indicates significance at the $p < 0.010$ level. No results were significant at the $p < 0.05$ level.

Topology	Unweighted	Transformed
Best	2307 (1 of 69 trees)	1044 (1 of 6 trees)
Hyriidae basal	2311 (0.6857, 1.0)	1044 (1.0, 1.0)
	2311 (0.7001, 0.9141)	1044 (1.0, 1.0)
		1044 (1.0, 1.0)
		1044 (1.0, 1.0)
		1044 (1.0, 1.0)
		1044 (1.0, 1.0)
Hyriidae + Etherioidea	2313 (0.5286, 0.9087)	1049 (0.3216, 0.3593)
	2313 (0.6599, 0.7545)	1049 (0.2513, 0.4545)
		1049 (0.2818, 0.3018)
		1049 (0.1967, 0.3877)
		1049 (0.0588*, 0.1250)
		1049 (0.1317, 0.2266)

that the null hypothesis that the data supports a constraint topology as well as the optimal topology is rejected at the 95% level. These tests are liberal, in that they can under-estimate p , providing false confidence in a particular optimal topology (Buckley et al., 2001). Nevertheless, in comparing the ability of COI to actually provide robust tests distinguishing alternative topologies, it performed poorly. Among the constraint trees tested, unweighted COI could not reject them, and transformed COI was able to distinguish only one of the six equally parsimonious “Hyriidae + Etherioidea” trees from the optimal topology (which in this case was one of the “Hyriidae Basal” trees) at the 90% level. Based upon these results and those of HBHC, transformed COI performs slightly better than unweighted COI, but neither performs well. This is reflected in the consistently low branch support for interfamilial relationships supported by COI (Graf & Ó Foighil, 2000; Bogan & Hoeh, 2000; Hoeh et al., 2001, 2002). We agree with HBHC that, when it comes to relying upon COI to recover such ancient divergences, “... we cannot objectively choose among interfamilial relationship hypotheses at this time” (p. 315).

However, COI is not the only dataset available to assess the most basal of freshwater mussel relationships, including the position of the Hyriidae. All morphological matrices analyzed to-date have provided the same result (when analyzed under parsimony): a sister relationship between the Hyriidae and the lasidium-bearing mussels (Graf, 2000; Hoeh et al., 2001; Roe & Hoeh, 2003). COI is equivocal on the subject of hyriid relationships, whereas morphology has been consistent in recovering a monophyletic Etherioidea that includes the Hyriidae – even when employing independently derived matrices.

The actual disagreement between G&C and HBHC in the case of the position of the Hyriidae (and perhaps the rest of the contentious branches on the freshwater mussel phylogeny) seems to be over whether or not the phylogenetic results to-date are robust enough to derive any conclusions, closing their discussion with (p. 315):

“Thus, robust estimates of unionoid bivalve (1) interfamilial relationships, (2) character evolution, and (3) lineage-specific species richness, as well as a stable, phylogeny-based

classification for the group, await appropriate phylogenetic analyses utilizing more inclusive datasets.”

We disagree: analyses to-date have been sufficiently robust to falsify a number of hypotheses, and even in the face of uncertainty and complexity, it is reasonable and useful to apply phylogenetic hypotheses as the tools that they are. These points get at the fundamental difference between our perspective and that argued by HBHC.

CONCLUSIONS

The goal of the G&C article was to put the classification of freshwater mussels on a cladistic foundation. Rather than being inductive and extrapolating generalities from the data, we set out to test hypotheses of the monophyly of the families, the interfamilial relationships, and the synapomorphies that support them. We used a combined evidence approach applying the available mtDNA, nuclear, and morphological datasets that had sufficient taxon sampling, and we drew upon the resulting phylogeny to meet our objectives. Moreover, our analyses were transparent – for example, we provided GENBANK accession numbers, museum vouchers, detailed descriptions of morphological characters, statistics of character-partition performance, and discussions of previous phylogenetic results. In addition, other unpublished materials (e.g., our complete matrix, results not shown) were made available on the MUSSEL Project Web Site – <http://www.mussel-project.net/>.

The G&C classification is a hypothesis to be tested. It has value only if it is useful as an organizing principle, a coherent evolutionary framework for freshwater mussel research. This is something that has been lacking despite more than a decade of cladistic analyses (Graf & Cummings, 2007) and something that the community has already put to good use (e.g., Barnhart et al., 2008; Rashleigh, 2008). But, the classification we proposed is just a hypothesis, and when it is shown to no longer be useful, it can be abandoned or modified. HBHC argue that COI is unreliable for testing interfamilial relationships of freshwater mussels. We agree, and that is why we did not rely solely on that limited set of characters. Moreover, G&C provided a conservative appraisal of the work to-date by not invoking ambiguous results to reject long-held hypotheses of relationship. HBHC have taken a bolder approach by introducing drastic

revisions to freshwater mussel classification, such as etheriid polyphyly and a novel subordinal classification (HBHC: fig. 2).

We regard the G&C classification of palaeo-heterodont families to be the best corroborated hypothesis of freshwater mussel relationships currently available. HBHC disagree. Based upon their concluding sentence (quoted above), it would seem that they are unsatisfied with the ability of any available phylogeny to distinguish among competing systems, although this is contradicted by their own proposed revisions. We expect that HBHC would agree with us that having a classification is preferable to none at all. Otherwise, if the plan is to suspend evolutionary considerations of freshwater mussel biology until the ultimate classification materializes *a posteriori* from the right (as yet unknown) combination of data and theory, we are afraid our efforts will have been wasted. Given the rapidly declining health of freshwater mussel populations around the world (Strayer, 2006) and our duty as systematists to provide a natural and useful classification for our stakeholders, the pressing problem of understanding the evolution and ecology of the Unionoida is too important to put off.

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NOMENCLATOR OF BIVALVE FAMILIES

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with a

CLASSIFICATION OF BIVALVE FAMILIES

by

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ABSTRACT

Some 1,048 names at the rank of subtribe, tribe, subfamily, family and superfamily have been proposed for Recent and fossil bivalves. All names are listed in a nomenclator giving full bibliographical reference, date of publication, type genus, and their nomenclatural availability and validity under the International Code of Zoological Nomenclature. Another 274 names, established for categories above the family-group are listed separately. A working classification attempts to group all bivalve family-group names into a single system based on current hypotheses of relations and synonymies. At several rank levels, the groups are given in alphabetical rather than some assumed phylogenetic arrangement, reflecting current uncertainties and conflicting results from anatomical, molecular, and fossil data.

Altogether, the classification recognizes as valid a total of 324 families, of which 214 are known exclusively as fossils and 110 occur in the Recent with or without a fossil record.

Key words: Bivalvia, nomenclature, taxonomy, taxon listing.

INTRODUCTION

The present volume on the nomenclature and classification of bivalve families follows an earlier one on gastropods also published in this journal (Bouchet & Rocroi, 2005). The context, rationale and organization of the two works are the same. Unlike for genus-group names, which are listed in general (Neave's Nomenclator Zoologicus) or specific (e.g., H. A. Vokes, 1980) nomenclators, a nomenclator of bivalve family-group names does not exist. It is thus difficult to establish their authorship and date, which of course determines priority. This, in addition to an incomplete understanding or application of the rules of nomenclature above genus level, contributes to nomenclatural instability. Even though he wrote before the cladistic revolution, Boss (1978) lamented that "The taxonomy of the Bivalvia is threatened by a cloying nomenclature both at specific and higher categorical levels." The purpose of the present paper is thus to provide verified bibliographical and nomenclatural data for

bivalve names in the family-group and above. The paper is organized in two parts: Part 1 is a nomenclator of 1,048 names that have been proposed for Recent and fossil gastropods at the rank of subtribe, tribe, subfamily, family and superfamily; 274 names established at ranks above the family-group are listed separately; Part 2 places these names in a classification.

The International Code on Zoological Nomenclature (4th edition) has set the conditions for the approval of a "List of Available Names" (Art. 79). Names entered in the List are deemed to have the date, availability, and other nomenclatural attributes given in the List. In addition, the List would be closed, that is names not entered in the List would be unavailable under the Code. The List would be approved in parts, and bivalve family-group names could constitute one such "Part of the List". We encourage users of the present publication to notify us with any omission and error they would notice, so that the present nomenclator, after amendments and corrections, could be submitted to ICZN to become an official Part of the List of Available Names in Zoology.

Part 1. NOMENCLATOR OF BIVALVE NAMES OF THE FAMILY-GROUP AND ABOVE

A Summary of the Rules of Nomenclature Applying to Family-Group Names

The International Code of Zoological Nomenclature (ICZN, 1999) defines the family group as including the taxa "at the ranks of superfamily, family, subfamily, tribe, subtribe, and any other rank below superfamily and above genus that may be desired" (Art. 35.1). Code regulations for names above the family group (sometimes

termed the class group) are few, but family-group names are subject to provisions which determine among others how the names shall be formed, their availability, and nomenclatural validity. Whereas some rules apply to all names in the species, genus and family groups, other rules apply specifically to family-group names. As these rules are sometimes little known or misunderstood, it may be appropriate to summarize how they affect family-group names.

Availability of Names

Articles 10–20 determine the conditions of availability of scientific names. Of specific relevance to this nomenclator of family-group names are Arts. 11.7 and 13.2, which state that:

- (1) “A family-group name when first published [...] must be a noun in the nominative plural formed from the stem of an available generic name [...]; the generic name must be a name then used as valid in the new family-group taxon” [Art. 11.7.1.1].

Examples:

Because *Caelonotus* (or *Caelonota*) was never established as a generic name, the name CAELONOTIDAE M’Coy, 1855, is not an available name.

The name SEPTIBRANCHIA was used by Grobben, 1892, as a family, and is not available as such because it is not formed from a genus name. (This does not affect its availability by those who want to use it above the rank of superfamily, as availability at such rank is not regulated by the Code).

Cossmann (1911) established the name LITHOPHAGELLIDAE based on *Lithophagella* Gray, 1854, but also treated *Lithophagella* as a synonym [of *Coralliophaga* Blainville, 1824], and thus not as a valid name. Under Art. 11.7.1.1 of the Code, LITHOPHAGELLIDAE is not an available name.

- (2) “A family-group name when first published must [...] be clearly used as a scientific name to denote a suprageneric taxon and not merely as a plural noun or adjective referring to the members of a genus” [Art. 11.7.1.2].

Da Costa (1776) appears to have been the first author who used the word “family” in a classification of the molluscs. Bouchet & Rocroi (2005: 5) concluded that his usage of family and genus names is inconsistent with the principles of Articles 4.1 [Names of taxon of rank higher than species group must consist of one word, whereas they occasionally consist of two words in Da Costa] and 11.7.1.2 of the Code. Da Costa’s classification was followed by Wilkes (1810), whose work has to be excluded from zoological nomenclature on the same grounds.

- (3) “A family-group name when first published must [...] not be based on certain names applied only to fossils and ending in the suffix *-ites*, *-ytes*, or *-ithes* [Art. 20]” [Art. 11.7.1.4].

Examples:

The genus name *Crassatellites* Krüger, 1823, was formed by adding the suffix *-ites* to the stem of the genus *Crassatella*, and was used to classify fossil species and thus distinguish them from extant members of that taxon. Under Art. 11.7.1.4, the family name CRASSATELLITIDAE Dall, 1895, is thus not an available name.

By contrast, *Batolites* Montfort, 1808, was clearly established as a new genus name, and not merely to indicate fossil members of another genus. The availability of the family name BATOLITIDAE Yanin, 1990, is thus unaffected by the provisions of Art. 11.7.1.4.

- (4) “If a family-group name was published before 1900, [...] but not in latinized form, it is available with its original author and date only if it has been latinized by later authors and has been generally accepted as valid by authors interested in the group concerned and as dating from that first publication in vernacular form” [Art. 11.7.2].

Examples:

“Sphaerulitidés” (French vernacular) of Douvillé, 1886 [published before 1900 but never latinized], is not an available name.

The author of LITHIOTIDAE is Cox, 1971, and not Reis, 1903, who established “Lithiotiden” a German vernacular name published after 1900, and thus not an available name.

Blainville (1814) used the French vernacular “Les mytilacées”. However, when Rafinesque (1815) established Mytilidae in the Latin form, he did not refer to Blainville’s vernacular name. Because the family name is now universally attributed to Rafinesque, 1815, it must not be attributed to Blainville, 1814.

The name ICHTHYOSARCOLITIDAE is universally attributed to Douvillé, 1887, who established it as the French vernacular “Ichthyosarcolitins”, although it was first latinized by MacGillavry, 1937.

The major difficulty in the application of this paragraph concerns names introduced mostly by French authors between 1800 and 1830. For example, Lamarck, Férussac, and Deshayes created numerous names in vernacular form that were often latinized by their translators and/or followers, notably Children, Goldfuss, and Bowdich. Many of these names are now accepted as valid in current classifications. The *Treatise on invertebrate paleontology* set a precedent by generally attributing their authorship and date

to their first establishment as a vernacular name, and we have accepted this usage in the present nomenclator.

(5) Description/Diagnosis.

Since the 1960 edition of the Code, Art. 13.1 requires that:

“To be available, every new name published after 1930 [...] must

13.1.1. be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon, or

13.1.2. be accompanied by a bibliographic reference to such a published statement [...]”.

Applicability of this rule to family-group names established after 1960 is unambiguous. Conversely, its application to names published after 1930 and before 1961 was, under the 1st, 2nd and 3rd editions of the Code, controversial (Bock, 1994). To leave some flexibility on this issue, the 4th edition of the Code now allows that “A family-group name first published after 1930 and before 1961 which does not satisfy the provisions of Article 13.1 is available from its original publication only if it was used as valid before 2000, and also was not rejected by an author who, after 1960 and before 2000, expressly applied Article 13 of the current editions of the Code” [Art. 13.2.1].

To summarize:

- before 1931: description or definition not necessary;
- after 1930 and before 1961: description or definition necessary, with exceptions ruled by Art. 13.2.1;
- after 1960: description or definition necessary, without exception.

Examples:

The name PERNOPECTININAE was established by Newell, 1938, without a description, and it was subsequently used before 2000 as valid by several authors, among others Nevesskaja et al. (1971), Scarlato & Starobogatov (1979a), and Amler (1999). PERNOPECTININAE Newell, 1938, is thus an available name.

By contrast, the name SOLECARDIIDAE Allan, 1950, which also was established without a description, was apparently never subsequently used as valid. It is thus not an available name.

The name LAEVICARDIINAE was established by Keen (1936: 367), without a description, and for that reason was rejected under Art. 13(a)(i) of the 3rd edition of the Code by Vidal (1994: 95). The name LAEVICARDIINAE is

available from Keen (1951: 7), who provided a description.

Because the name CUNIDAE was established after 1960 by Iredale & McMichael (1962) without a description or definition, it is unavailable from that publication. CUNINAE is available from Chavan, in Moore, 1969, who gave a definition.

(6) Conditional proposal.

“A new name or nomenclatural act proposed conditionally and published after 1960 is not thereby made available” [Art. 15.1].

Example:

In a discussion on the family Edmondiidae, Waterhouse (1969: 28) stated that “*Myonia* and allies possibly belong to a distinct tribe, distinguished from *Edmondia* by [description follows]. In the text, that tribe is not named, but the name “Tribe Myoniides” appears on his figure 9, p. 21. We have considered that under Art. 15.1 the name MYONIIDI is not available from Waterhouse, 1969.

Formation of Names

Articles 25–34 determine the formation and treatment of names. Of specific relevance to family-group names are Articles 29 [Formation of family-group names] and 32 [Original spellings].

The suffixes for names at the ranks of superfamily, family, subfamily, tribe and subtribe are regulated by Art. 29.2 (Table 1). The suffix -oidea for superfamily, which had only been a Recommendation in the 3rd edition of the Code, is now mandatory in the 4th edition.

Article 32.5.3 states that:

“A family-group name is an incorrect original spelling and must be corrected if it

32.5.3.1. has an incorrectly formed suffix [Art. 29.2], or

32.5.3.2. is formed from an unjustified emendation of a generic name (unless the unjusti-

TABLE 1. Suffixes for family-group names.

Rank	Suffix	Example
Superfamily	-OIDEA	CARDIOIDEA
Family	-IDAE	CARDIIDAE
Subfamily	-INAE	LYMNOCARDIINAE
Tribe	-INI	LYMNOCARDIINI
Subtribe	-INA	LYMNOCARDIINA

fied emendation has become a replacement name), or

32.5.3.3. is formed from an incorrect subsequent spelling of a generic name [Art. 35.4.1]; or

32.5.3.4. is formed from one of two or more original spellings of a genus-group name not selected by the First Reviser [Art. 24.2.3]".

"An incorrect original spelling has no separate availability in the original form and cannot, in that form, enter into homonymy or be used as a replacement name" [Art. 32.4].

Examples:

The family rank name MYOPHORIEAE Bronn, 1849, has an incorrectly formed suffix and must be corrected to MYOPHORIIDAE.

KELLYELLIDAE P. Fischer, 1887, is formed from *Kellyella* P. Fischer, 1887, an unjustified emendation of *Kelliella* M. Sars, 1870. KELLYELLIDAE is an incorrect original spelling that must be corrected to KELLIELLIDAE.

Auporia is an incorrect subsequent spelling of *Aupouria* Powell, 1937, and AUPORIIDAE Scarlato & Starobogatov, 1979, is an incorrect original spelling that must be corrected to AUPOURIIDAE.

Article 29 states that: "A family-group name is formed by adding to the stem of the name of the type genus [Art. 29.3], or to the entire name of the type genus [Art. 55.3], a suffix as specified in Article 29.2" [Art. 29.1].

The stem of the names of type genera is determined by Art. 29.3 in accordance with the rules of Latin grammar. The first, second and third editions of the Code ruled that a family-group name with a wrongly formed stem was an incorrect original spelling that must be corrected. However, the 4th edition of the Code now rules that:

"If a spelling of a family-group name was not formed in accordance with Article 29.3 but is in prevailing usage, that spelling is to be maintained, whether or not it is the original spelling and whether or not its derivation from the name of the type genus is in accordance with the grammatical procedures in Articles 29.3.1 and 29.3.2" [Art. 29.5].

The purpose of Art. 29.5 is to avoid destabilizing family-group names in current use by requiring mandatory changes for purely grammatical reasons. In the discussion preceding the publication of the 4th edition of the Code, the issue of adherence to the rules of the Latin grammar has seen the scientific community split.

Some scientists see this adherence as part of the scholarship of their profession, others see it as an outdated remnant of the epoch when zoologists had training in Latin and Greek. Although we have ourselves had that training, we do not want to impose our vision to the community of bivalve systematists, and we have followed the spirit of Art. 29. Ultimately, the question is whether we have stability in the spelling of bivalve family-group names, and whether following the "grammatical niceties" (Wheeler, 1990) in Article 29.3 would do more harm than good. It seems that the spelling of bivalve family-group names is an issue that has attracted little attention so far and, after conferring with a number of colleagues, we have concluded that for a vast majority of the names there is no such thing as a "prevailing usage" that should eventually be maintained against the rules of Latin grammar. Many colleagues in fact suggested that the present nomenclator would probably become the standard reference for bivalve family-group names and that one of its consequences would be precisely to settle such nomenclatural issues. In this nomenclator, we have been guided principally by adherence to the rules of Latin grammar [Art. 29.3], except where such adherence would contravene with the spirit of Art. 29.5.

We have also been guided by consistency. We believe that consistently deriving family-group names formed on genera with similar endings offers advantages in memorizing the names. For instance, the family-group names based on *Mesodesma* and *Lyrodesma* were originally spelled MESODESMIDAE (incorrectly formed) and LYRODESMATIDAE (correctly formed). However, as both generic names have the same stem (the genitive of *desma* is *desmatis*, and the stem is *desmat-*), it is easier to memorize the consistently formed family-group names MESODESMATIDAE and LYRODESMATIDAE, and we have chosen to correct MESODESMIDAE to MESODESMATIDAE. The same holds for the family-group names formed on *Aviculopecten* and *Tosapecten*, which we have accepted to be AVICULOPECTINIDAE and TOSAPECTINIDAE, rather than AVICULOPECTINIDAE (correctly formed original spelling) and TOSAPECTENIDAE (incorrectly formed original spelling). (The genitive of *pecten* is *pectinis*, and the stem is *pectin-*).

Conversely, the rules of Latin and Greek grammar appear to have consistently been ignored in the formation of family-group names deriving from genera with the suffix *-opsis*. Although the rules would recommend family name endings in -OPSEIDAE, the prevailing usage are endings

in -OPSIDAE, and we have not attempted to correct this.

We have tabulated the formation of family-group names derived from the most commonly encountered endings of a generic name (Table 2).

Validity

The taxonomical validity of a nominal taxon is determined subjectively by the opinion of individual taxonomists. An author may consider that two nominal family-group names are valid when another author may consider them the same taxon, with one name a junior synonym of the other. Taxonomical validity is not determined by the Code and is not considered in this nomenclator.

Nomenclatural validity is a different issue that is determined objectively by the application of the Code. Validity is determined by Art. 23 [Principle of Priority] and 24 [Principle of the First Reviser], as well as parts of Arts 35–41 [Family-Group Taxa and Names]. Of particular relevance to this nomenclator are the following Articles.

- (1) “The name of a family-group taxon is invalid if the name of its type genus is a junior homonym or has been suppressed by the Commission” [Art. 39].
Examples:
The name MICRODONTELLIDAE Gusev, 1969, is invalid because its type genus *Microdontella* Lebedev, 1944, is a junior homonym of *Microdontella* Strand, 1934.
The name GLYCIMERIDAE Bronn, 1849, is invalid because its type genus *Glycimeris* Lamarck,

1799, has been placed by Opinion 1414 on the Official Index of Rejected and Invalid Generic Names in Zoology.
However, “Homonymy between family-group names may result from similarity but not identity of the names of their type genera” (Art. 55.3). “Such a case [...] must be referred to the Commission for a ruling [...]” (Art. 55.3.1).

Example:
The name ASAPHIDAE Winckworth, 1932, based on *Asaphis* Modeer, 1793, is a homonym of ASAPHIDAE Burmeister, 1843, based on *Asaphus* Brongniart in Brongniart & Desmarest, 1822 [Arthropoda]. The bivalve family name is not invalid, but requires a ruling from the Commission to emend its spelling to, e.g., ASAPHISINAE.

- (2) “When the name of a type genus of a nominal family-group taxon is considered to be a junior synonym of the name of another nominal genus, the family group name is not to be replaced on that account alone” [Art. 40.1].
Example:
H. A. Vokes (1967) placed *Trechmanella* Cox, 1933, in synonymy of *Anomoptychus* Douvillé, 1906, and replaced TRECHMANELLIDAE Cox, 1934, with the new name ANOMOPTYCHIDAE. This replacement is unjustified under the Code and the nomenclaturally valid name of the family-group taxon containing *Trechmanella* and *Anomoptychus* is TRECHMANELLIDAE.
- (3) “If, however, a family-group name was replaced before 1961 because of the synonymy of the type genus, the replacement name is

TABLE 2. Most common bivalve generic suffixes and the formation of derived family-group names.

Generic ending	Meaning	Derived family name		Example	
		ending	Genus		Family
-chlamys	mantle (Greek)	-CHLAMYDIDAE	<i>Mimachlamys</i>		MIMACHLAMYDINAE
-concha	shell (Greek/Latin)	-CONCHIDAE	<i>Jilinoconcha</i>		JILINOCONCHIDAE
-dens	tooth (Latin)	-DENTIDAE	<i>Rectidens</i>		RECTIDENTIDAE
-desma	hinge (Greek)	-DESMATIDAE	<i>Afghanodesma</i>		AFGHANODESMATIDAE
-donta	tooth (Greek)	-DONTIDAE	<i>Ctenodonta</i>		CTENODONTIDAE
-mya	clam (Greek)	-MYIDAE	<i>Vesicomya</i>		VESICOMYIDAE
-odon	tooth (Greek)	-ODONTIDAE	<i>Grammatodon</i>		GRAMMATODONTIDAE
-pecten	comb (Latin)	-PECTINIDAE	<i>Aviculopecten</i>		AVICULOPECTINIDAE
-pteria	wing (Greek)	-PTERIIDAE	<i>Leiopteria</i>		LEIOPTERIINAE
-risma	edge (Greek)	-RISMATIDAE	<i>Pachyrisma</i>		PACHYRISMATIDAE
-unio	pearl (Latin)	-UNIONIDAE	<i>Americunio</i>		AMERICUNIONINAE

to be maintained if it is in prevailing usage. A name maintained by virtue of this Article retains its own author but takes the priority of the replaced name of which it is deemed to be the senior synonym" [Art. 40.2].

Examples where Art. 40.2 does not apply:

Finlay (1928) placed *Paphia* Röding, 1798, and *Tapes* Megerle von Mühlfeldt, 1811, in the same family. He did not treat them as synonyms but, because *Paphia* was the senior name, he established the new name PAPHIINAE in place of TAPETINAE Gray, 1851. PAPHIINAE is not a replacement name in the sense of Art. 40.2, and it does not take the priority of TAPETINAE.

Dall (1894) established PTEROPSINAE based on *Pteropsis* Conrad, 1860. However, the type genus is a junior homonym of *Pteropsis* Rafinesque, 1814 [Cnidaria]. H. A. Vokes (1956b) and Keen, in Moore (1969) replaced *Pteropsis* and PTEROPSINAE with the names *Pteropsella* and PTEROPSELLINAE respectively. The replacement was not a consequence of synonymy of the type genus and Art. 40.2 does not apply.

Examples where Art. 40.2 applies:

Stoliczka (1870) placed *Amphidesma* Lamarck, 1818, in synonymy of *Semele* Schumacher, 1817, and replaced AMPHIDESMATIDAE Latreille, 1825, with the new name SEMELINAE. SEMELINAE is in prevailing usage, is to be maintained, and takes the priority of AMPHIDESMATIDAE. It should be cited SEMELINAE Stoliczka, 1870 (1825).

Beyond such cases that fit literally to the wording of the Code, there is a broader array of cases in which the author establishing the younger family-group name did not explicitly state that he did so "because of the synonymy of the type genus".

For instance, when he established the name GLOSSIDAE, Gray (1847b) did not state that he was replacing ISOCARDIIDAE Gray, 1840, because of the synonymy of *Isocardia* Lamarck, 1799, nor did he even mention the name ISO-CARDIIDAE, but he cited *Isocardia* as a synonym of *Glossus* Poli, 1795. We have treated this as a situation covered by Art. 40.2. GLOSSIDAE is in prevailing usage and is to be maintained, with the precedence of ISOCARDIIDAE. It should be cited GLOSSIDAE Gray, 1847 (1840).

Departing still a little further from the letter of Art. 40.2, there are cases in which the author establishing the younger family-group name not only did not explicitly stated that he was doing so "because of the synonymy of the

type genus", but did not even mention the synonymy of the genera involved.

For instance, when he established CLEIDOTHAERIDAE, Hedley (1918) did not state he was replacing CHAMOSTREIDAE Stoliczka, 1870, because of the synonymy of *Chamostrea* Gray, 1840, nor did he mention the names CHAMOSTREIDAE or *Chamostrea*. However, *Cleidothera* Stutchbury, 1830, and *Chamostrea* are synonyms, and CLEIDOTHAERIDAE is in prevailing usage. We have also treated this as a situation covered by Art. 40.2, and we have maintained CLEIDOTHAERIDAE Hedley, 1918 (1870), as the valid name.

Names that are invalid under Art. 39, or because they have been placed on the Official Index, are permanently invalid, and cannot be used as valid in any classification. Taxonomical synonyms are also invalid, but only within the frame of a classification, and these may be resurrected by another author who has a different opinion about classification.

Example:

Our classification recognizes a superfamily SOLEMYOIDEA with a single family, with three subfamilies and one synonym:

Family SOLEMYIDAE Gray, 1840

SF SOLEMYINAE Gray, 1840 [= Janacekiidae Růžicka & Řehoř, 1978]

SF ACHARACINAE Scarlato & Starobogatov, 1979

†SF CLINOPISTHINAE Pojeta, 1988

A hypothetical author recognizing more family-level taxa within the superfamily could come with another classification, e.g.:

Family SOLEMYIDAE Gray, 1840

SF SOLEMYINAE Gray, 1840 [= Janacekiidae Růžicka & Řehoř, 1978]

†SF CLINOPISTHINAE Pojeta, 1988

Family ACHARACIDAE Scarlato & Starobogatov, 1979

Principle of Coordination

Article 36 states that "A name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date for taxa based upon the same name-bearing type (type genus) at other ranks in the family group, with appropriate mandatory change of suffix".

Example:

Habe (1977) established the name CAMP-TONECTINAE at subfamily rank. He is deemed to have established that name at any other rank in the family group. The author and date

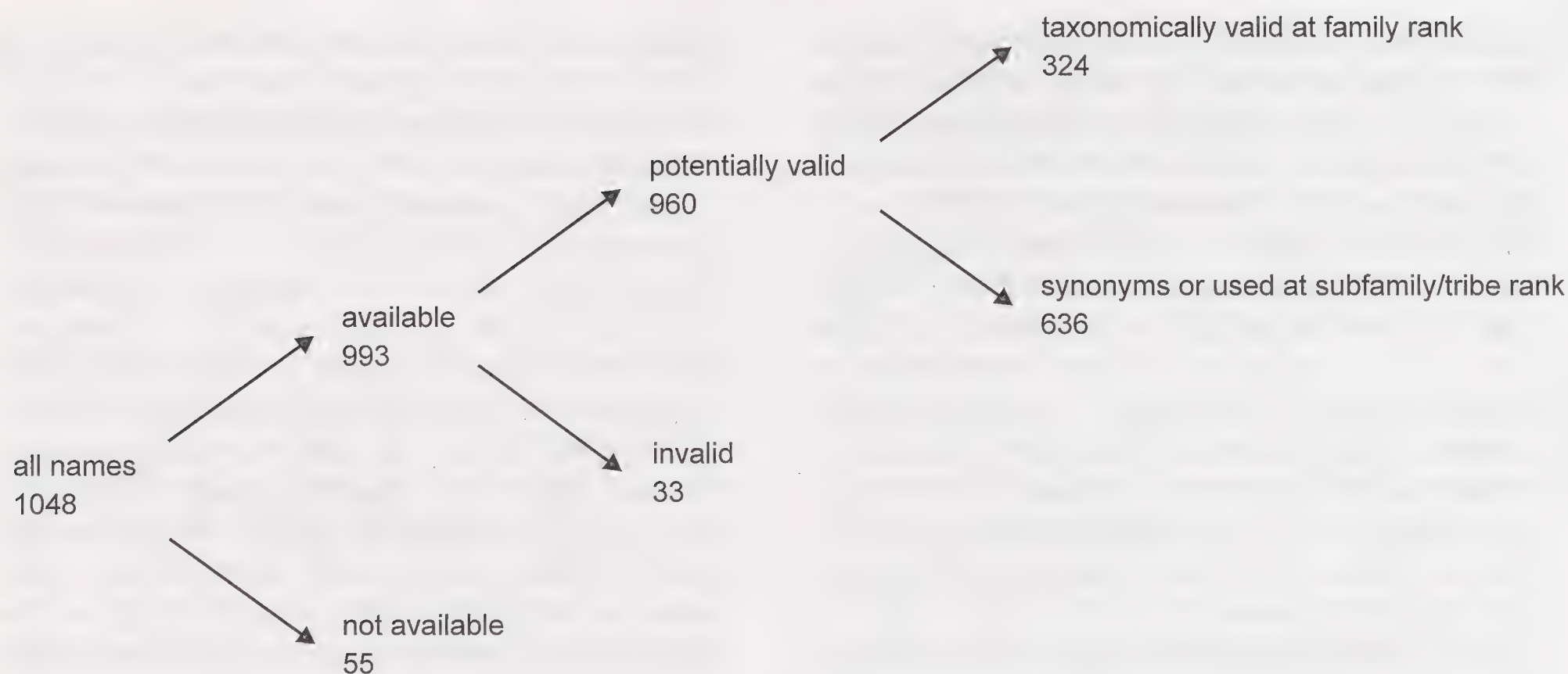


FIG. 1. How the nomenclatural and taxonomical filters operate on the 1,048 names established or used for bivalve families, subfamilies, or tribes.

of CAMPTONECTIDAE is Habe, 1977, despite that it was declared a new family by Dickan (1991).

Status of Names in the Official List of Family-Group Names in Zoology

Nineteen bivalve family-group names have been placed on the *Official List* by the Commission of Nomenclature, and 5 have been placed on the *Official Index*. The Code rules that "The status of a name entered in an *Official List* is subject to the ruling(s) in any relevant Opinion(s) [...]; all other aspects of its status derive from the normal application of the Code" (Art. 80.6.2) and also that "A name may be placed in an *Official List* without any additional qualification" (Art. 80.6.3).

We have found 8 instances in which the authorship and/or date of publication of a name entered on the *Official List* or *Official Index* are erroneous, that is that name has been established earlier by the same or another author.

Cases to be Submitted to the Commission

Inevitably, a review of family-group names such as the present one has made apparent a number of nomenclatural cases that cannot be solved without a decision of the Commission. The problems are simply discussed under the appropriate headings in the Nomenclator or in the Appendices. It was felt inappropriate to prepare applications for publication in the *Bulletin of Zoological Nomenclature* before

publication of the present work, because it is precisely the purpose of the present work to highlight the problems, elicit discussion and seek a consensus among malacologists. A solution to all these problems will probably take several years. Ultimately, the present Nomenclator could, after amendments, become a Part of the *List of Available Names in Zoology*, as regulated by Article 79 of the Code.

Nomenclator

Growth in Numbers of Bivalve Family-Group Names

A total of 1,048 names at the rank of subtribe, tribe, subfamily, family, and superfamily have been proposed for Recent and fossil bivalves, or have, at one time or another, been used at these ranks. (Names established for fossils now classified in Rostroconchia are not included in these and the following statistics). Of these, 55 are not available names, mainly because they are not based on a genus name. This leaves 993 names that meet the criteria of availability. Of these, 30 are permanently invalid, mainly because the type genus is a junior homonym; when these are eliminated, there are 960 names that are potentially valid (Fig. 1).

An analysis of the year of publication of the 960 potentially valid names shows (Fig. 2) that, on average, 1.2 names have been established yearly in the period 1800–1839, 3.4 in the period 1840–1959, and 10.1 since 1960. As for the gastropods, three above average periods

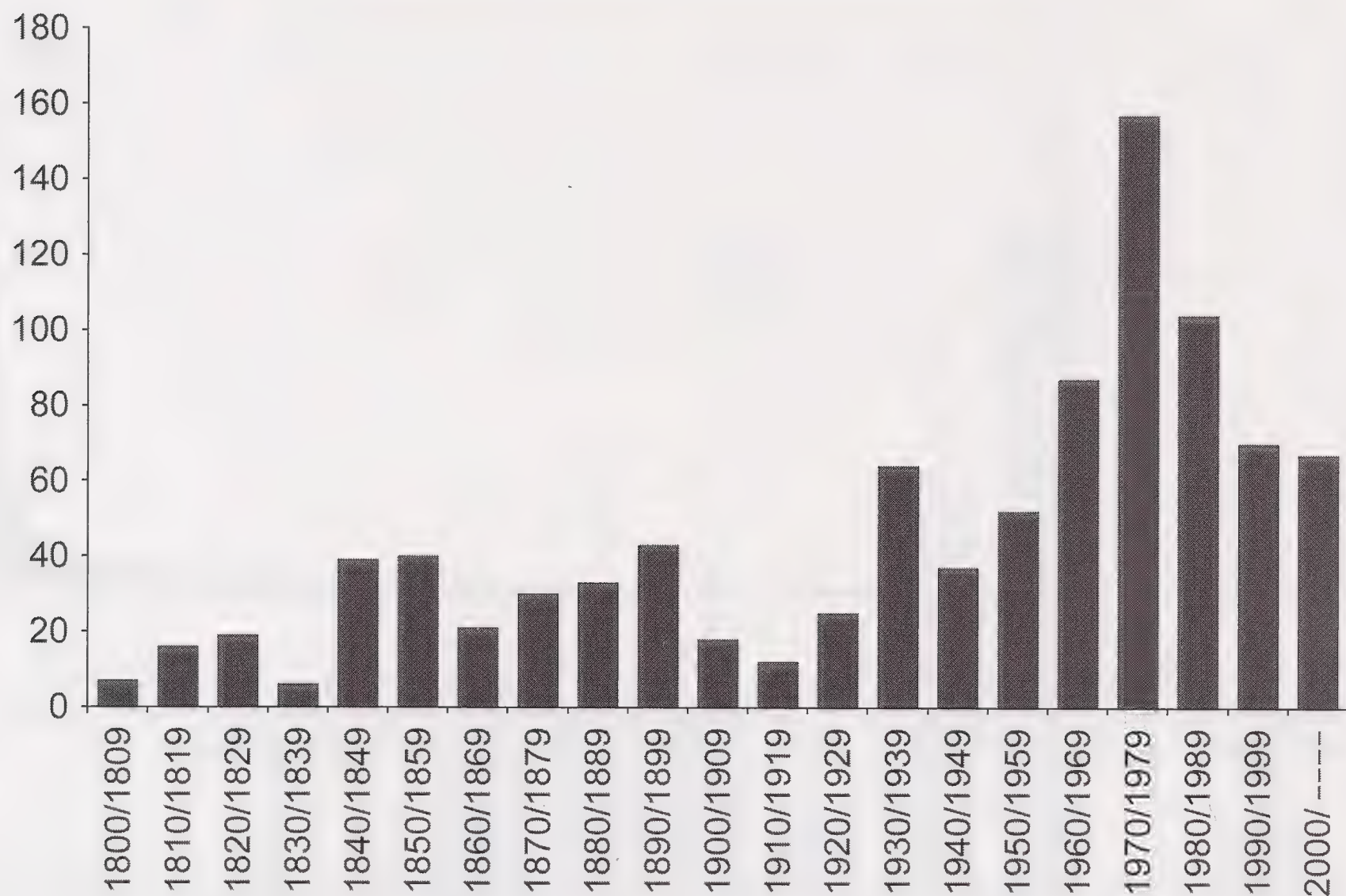


FIG. 2. Number of available names (total 984) published during each decade since 1800.

stand out, but the details differ: a broad swelling in the 1840–1850s; a narrower peak in the 1930s; and a sharp and sustained increase marking modern times, with a peak in the 1970s (Bouchet & Rocroi, 2005).

The first peak corresponds essentially to four authors: Gray, notably the successive editions of the *Synopsis of the contents of the British Museum* (1840b, 1842), his *List of genera of Recent Mollusca* (1847b) and *Figures of molluscan animals* (1857b); d'Orbigny's *Voyage dans l'Amérique méridionale* (1835–1847), *Paléontologie française* (1844–1848), and other publications; Deshayes' *Catalogue of the Conchifera* (1853, 1854); and finally H. Adams & A. Adams' *Genera of Recent Mollusca* (1854–1858). The last two decades of the 19th century saw the publication of Paul Fischer's *Manuel de conchyliologie et de paléontologie conchyliologique* (1880–1887), S. A. Miller's *North American geology and palaeontology* (1889), Ulrich & Schofield's paleontology of Minnesota (1894), and Dall's new classification of the Pelecypoda in his *Contributions to the Tertiary fauna of Florida* (1895a). The first three decades of the 20th century are calm, until the 1930s when many authors together contribute to the establishment of new family names for fossil (Cox, Heinz, MacGillavry, MacNeil, Mailieux, Newell, Stewart, Vialov) and, to a lesser extent, Recent (Iredale, Thiele) bivalves. Start-

ing in the 1960s, there is an intense bivalve taxonomic activity that continues to this day. Eberzin's *Osnovy paleontologii* (1960) marks the importance of the Soviet/Russian school, which is alone responsible for about half of the new names (and Starobogatov accounting for 107 names, mostly in co-authorship with Scarlato) and numerous contributions from Astafieva, Betekhtina, Kafanov, Kasum-Zade, Kolesnikov, Nevesskaja, Paramonova, Vialov, Yanin and others, each specializing on a section of the bivalve tree and/or a basin or geological period. In North America, publication of the bivalve part of the *Treatise on invertebrate paleontology* (Moore, 1969) was probably the first attempt of a collective reference work by authors originating from several countries, and even several continents. In the four decades that followed, publications by authors from the U.S.A. (Carter, Harry, Keen, Newell, Pojeta, H. A. Vokes, Waller and others) represent the second largest source of new bivalve families. In China, publication of several regional atlases, among others, was the source of new fossil bivalve families by Zongjie Fang, Zhiwei Gu, Fuxiang Guo, Benpei Liu, Xiezhong Liu, Qihong Ma, Jingeng Sha, Renjie Zhang and others. Finally, this overview of modern publication statistics would not be complete without singling out the standing-alone contributions and fecundity of Bruce Waterhouse.

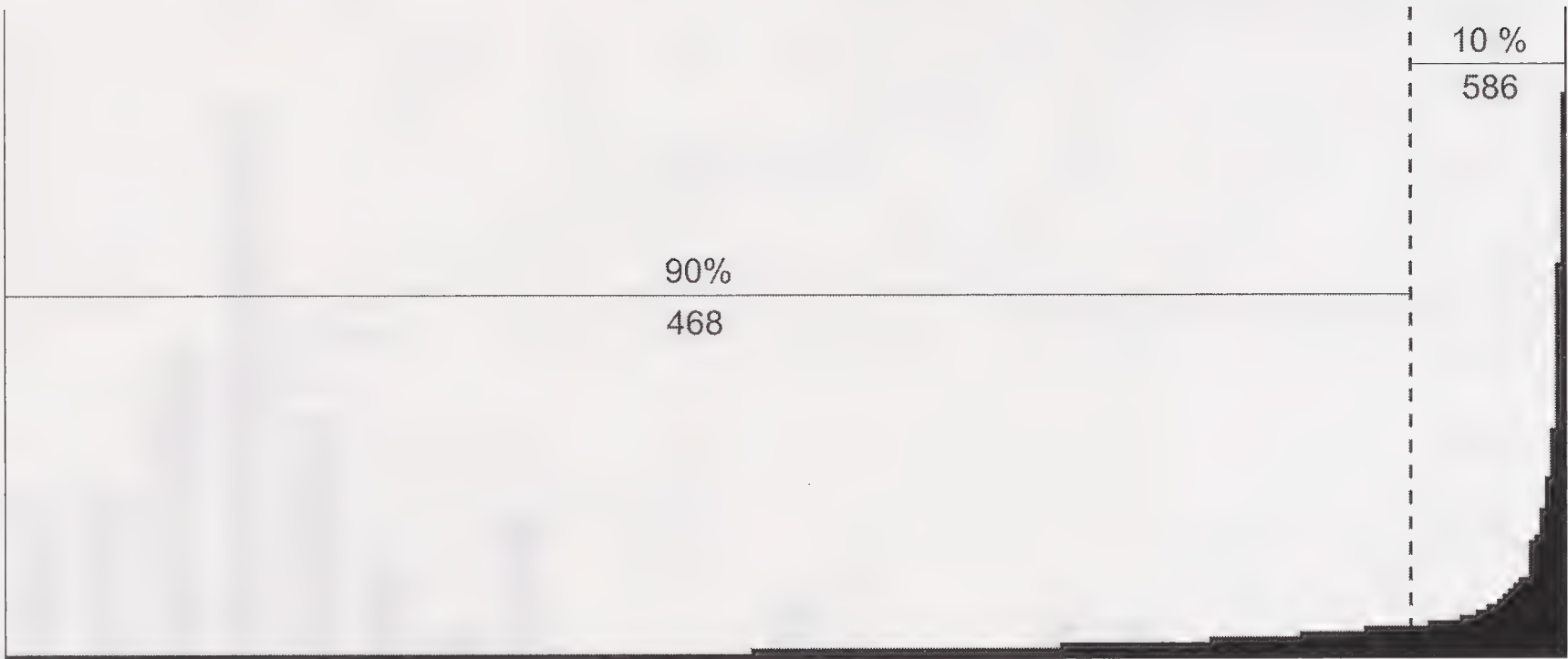


FIG. 3. Ranking of author-name pairs (total 1,054) by number of names published by author. To the left of the histogram, many authors are responsible for single author-name pairs; to the right, Starobogatov alone is responsible for 107 names (Table 3).

The 960 potentially valid names involve a total of 293 authors or co-authors, and there are 1,054 author-name pairs (as a name can have more than one author). 48% of authors appear only once, 90% of the authors are responsible for 45% of the pairs, and 10% of the authors are responsible for 55% of the names (Fig. 3; Table 3). Interestingly, only two of the most prolific authors (Gray and Starobogatov) were also among the top 10 most prolific authors for gastropod family-group names.

533 available names (56.5%) are based on genera with a fossil type species. This is a notable difference with gastropods, where only 23% of the names were based on such genera with a fossil type species. There are two reasons that explain

this difference. First, nearly one-fourth (24.6%) of all valid gastropod families occurring in the Recent are slugs, that do not leave a fossil record. Second, bivalves are better preserved in the fossil record than gastropods. In the Paleozoic, there is a steady increase in the number of bivalves families from Cambrian to Carboniferous, and the Permian crash observed in gastropods is not seen in the bivalves (Fig. 4). In the Mesozoic, there are many more names with a Cretaceous type species than for any other pre-Tertiary period, again a difference with gastropods where Jurassic type species were the majority.

Altogether, the classification recognizes as valid a total of 324 families, that is 34% of all 960 potentially valid family-group names. The other 66% are either synonyms or used as valid at lower ranks (subfamilies, tribes). There are few standard works that have covered all bivalve clades, Recent and fossil. With 324 families, the present classification has the highest number ever considered valid (Table 4): this is more than 3 times as many as in Fischer’s *Manuel de conchyliologie*, 120 years ago. Of the 324 valid families, 214 are known exclusively as fossil and 110 occur in the Recent with or without a fossil record.

Format of the List

The nomenclator of bivalve family-group names presents the following information:

- (1) NAME author, year [day, month]
- (2) Reference
- (3) Type genus
- (4) Remarks

TABLE 3. The ten authors responsible for establishing the largest number of bivalve family-group names.

Author	Number of new family-group names
Starobogatov	107
Scarlato	74
Gray	45
Waterhouse	34
Dall	28
Newell	23
S.A. Miller	16
Rafinesque	15
Habe	15
P. Fischer	14

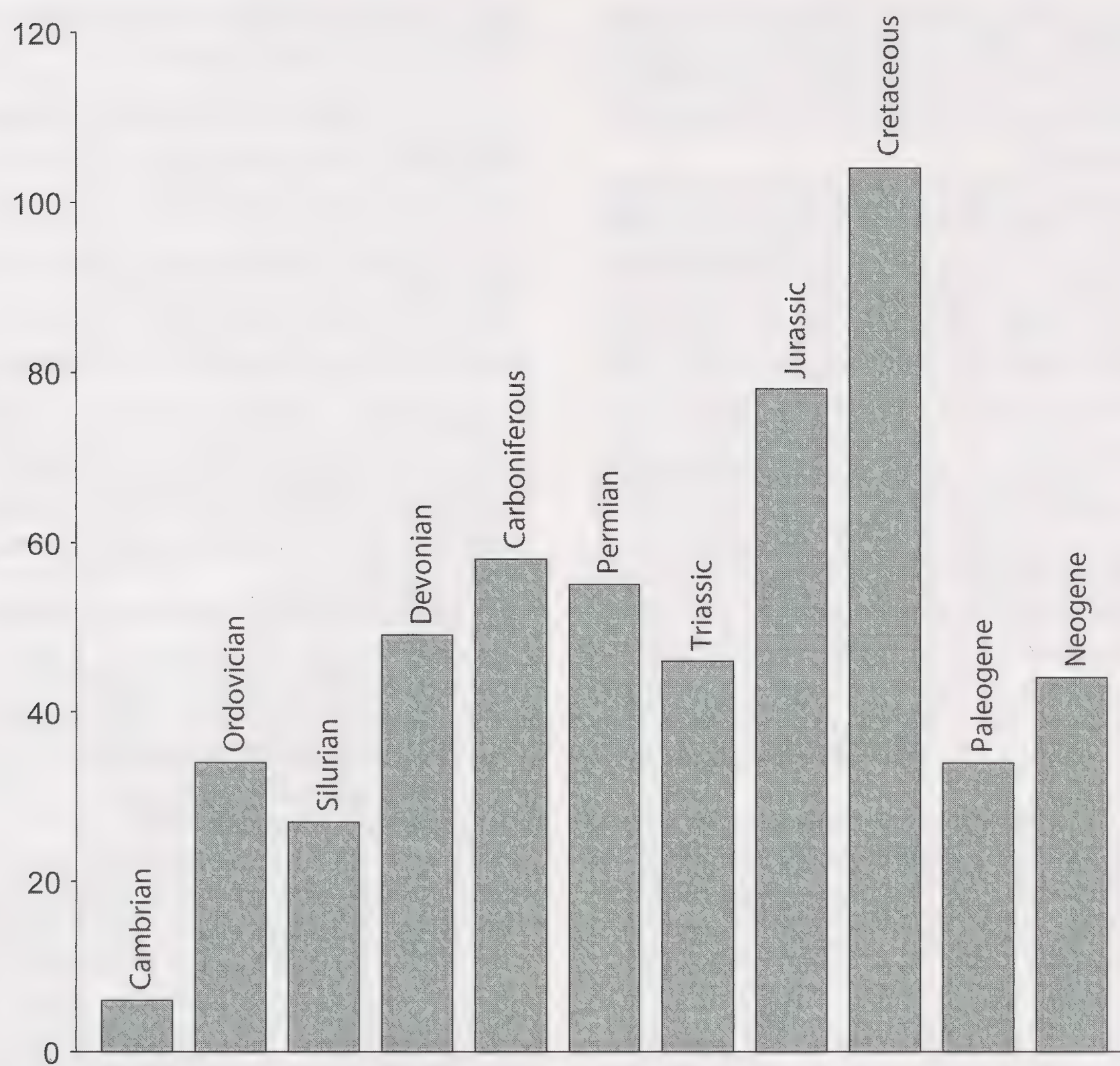


FIG. 4. Number of available family-group names (total 533) based on genera with a fossil type species, ranked by geological age of the type species.

(1) In the case of authors with identical family names (e.g., Adams, Fischer, Miller, Morris), we have added initials. In the case of Chinese authors, we give under “Reference” their full name as recommended by Xu & Nicolson (1992). For German authors, we

have followed German usage and have omitted the nobiliary particles from the author’s name. This usage does not apply to Dutch names, which retain their nobiliary particles, for example van de Poel (alphabetized under van de Poel). For French authors, we

TABLE 4. Number of Recent and fossil bivalve families treated as valid in selected standard references.

Work	Author(s)	No. of families
Manuel de conchyliologie	P. Fischer (1886–1887)	89
Osnovy Paleontologii	Eberzin (1960)	118
Traité de Zoologie	Franc (1960)	147
Treatise on Invertebrate Paleontology	Moore, ed. (1969)	248
The Fossil Record	Skelton & Benton (1993)	225
	Amler (1999)	269
Present work		324

have followed prevailing usage, for example d'Orbigny, Lamarck and Blainville, rather than de Lamarck and de Blainville (alphabetized under Orbigny, d', Lamarck, and Blainville, respectively).

Precise dates of publication, to the month and day, have been searched in available published sources (often bio-bibliographies of authors) or obtained from the covers of journals. In the case of Soviet era materials, we have taken the "podpisano" as the earliest possible date of publication, and we have indicated this as "after ["podpisano"] date". (The "podpisano" is the approval for printing by publication authorities; it appears on the last printed page of a book, together with other information such as number of print copies). Russian colleagues (Y. Kantor, A. Sysoev, pers. com.) indicate that publications were usually printed within weeks after the "podpisano" date, although in some cases (not involved here) publication was delayed by years.

When a name takes its precedence from a senior unused synonym under Art. 40 of the Code, the inherited date of precedence appears in parenthesis (Recommendation 40A of the Code).

- (2) Bibliographical references. We give in full the title of the journal or the series; in the case of series with complex volume numbering, we indicate explicitly the name of parts (for example, Theil, Band, Heft). To standardize, the expression "new ser." (new series) is used also for journals in languages other than English in place of, for example, "Neue Folge" (German), "nouvelle série" (French).
- (3) Type genus. A dagger (†) before the name of a type genus indicates that its type species is a fossil.
- (4) The "Remarks" contains such information as: original spelling [if an incorrect original spelling under Art. 32] and history of the name [if originally published as a vernacular name]; nomenclatural availability and validity; references to changes of rank.

Changes of Rank: Notwithstanding the Principle of Coordination [Art. 36], we have attempted to trace the changes in rank that each family-group name underwent. This is the concept of *nomen translatum* that was consistently used in the *Treatise on invertebrate paleontology*. Under Art. 36, a change of rank in the family

group does not affect the author and date of the name with modified suffix.

The literature containing changes of rank is much larger than the primary literature containing new family-group names, and we have probably missed a good number of changes. We would like to stress, however, that this does not affect the nomenclature of taxa, but merely their subsequent taxonomical use.

The rank of a family-group name is that attributed to it by an author in a classification or in a heading. However, when the author has used ranks in a meaning different from current usage, we have considered the rank that was intended rather than the rank nominally attributed by the author. A few specific cases need to be singled out:

- (a) Cossmann (1906) used the word "cénacle" in reaction to the usage of "superfamille", which he disliked on vocabulary grounds (he ridiculed the word "superfamille" which he compared to "superprésident"!). We have naturally regarded Cossmann's cénacles as equivalent to superfamilies.
- (b) Thiele (1925–1926) used the word "Sippe" and (1929–1935) the word "Stirps" for taxa at a rank above family and below order. Many of these, but not all, are formed on a genus name and have a suffix in -acea. Thiele's Sippe and Stirps have generally (for example, Bieler & Mikkelsen, 1992) been regarded as equivalent to superfamilies and we have followed this interpretation here.

Nomenclator of Bivalve Family-Group Names

ABIELLIDAE Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinentalnykh vodoemov zemnogo shara*: 76

Type genus: †*Abiella* Khalfin, 1950 [not available from Ragozin, 1933 (no type species designated)]

ACANTHOCARDIINI Kafanov & Starobogatov, 1977

Reference: [in Kafanov & Popov] *Paleontologicheskii Zhurnal*, 1977(3): 63

Type genus: *Acanthocardia* Gray, 1851

ACANTHOPECTINIDAE Newell & Boyd, 1995 [13 December]

Reference: *Bulletin of the American Museum of Natural History*, 227: 45

Type genus: †*Acanthopecten* Girty, 1903

Remarks: -inae, Waterhouse (2008: 153).

ACHARACIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*, 80: 19, 26

Type genus: *Acharax* Dall, 1908

Remarks: -oidea, same reference; -inae, Bieler, Carter & Coan, herein.

ACOBAECARDIINI Paramonova, 1986
Reference: [in Nevesskaja et al.] *Trudy Paleontologicheskogo Instituta*, 220: 192

Type genus: †*Acobaecardium* Paramonova, 1986

Remarks: -ina, Bieler, Carter & Coan, herein.

ACOSTAEIDAE Morrison, 1973 [23 March]
Reference: *Bulletin of the American Malacological Union*, 38: 45

Type genus: *Acostaea* d'Orbigny, 1851

ACTINODESMATINAE Maillieux, 1920
Reference: *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie*, 29: 149

Type genus: †*Actinodesma* Sandberger, 1856

Remarks: Original spelling Actinodesminae. -idae [declared new], Scarlato & Starobogatov (1979a: 20).

ACTINODONTIDAE Davies, 1933 [15 November]
Reference: *Proceedings of the Malacological Society of London*, 20(6): 323

Type genus: †*Actinodonta* Phillips, 1848

Remarks: Original spelling (superfamily) Actinodontacea; name only, no description, but available because it was used as a valid name before 2000, e.g. Babin (1966: 228, Latin name attributed to Douvillé). Not available from "Actinodontidés" (vernacular) of Douvillé (1913: 438). Declared new, and diagnosed, as -idae and -oidea, by Scarlato & Starobogatov (1979a: 20, 26). Homonym of Actinodontidae Lydekker, 1885, based on *Actinodon* Gaudry, 1867 [Amphibia].

ACTINODONTOPHORIDAE Newell, 1969
Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 468

Type genus: †*Actinodontophora* Ichikawa, 1951

Remarks: -oidea, Nevesskaja et al. (1971: 14).

ACTINOPTERELLINAE Maillieux, 1931 [31 December]

Reference: *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 51: 62

Type genus: †*Actinopterella* Williams, 1908

ACUTICOSTINAE Starobogatov, 1967
Reference: *Trudy Vsesoiuznogo Paleontologicheskogo Obshchestva*, 9: 178

Type genus: *Acuticosta* Simpson, 1900

ADACNIDAE Gill, 1871 [February]
Reference: *Smithsonian Miscellaneous Collections*, 227: 20

Type genus: *Adacna* Eichwald, 1838

Remarks: -inae, Eberzin (1965: 18); -ini, Nevesskaja, Paramonova & Popov (2001: 207). See also Hypaninae.

ADAMUSSIINAE Habe, 1977
Reference: *Systematics of Mollusca in Japan (Bivalvia and Scaphopoda)*: 75

Type genus: *Adamussium* Thiele, 1934

Remarks: Original spelling Adamussinae. -ini, Beu & Darragh (2001: 2, 13, 121).

ADAPEDONTA
See higher category list.

ADELOSIPHONIA Dall, 1895 [March]
Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 532

Remarks: Established as a section of the superfamily Laternuloidea, including the families Pandoridae and Cleidothaeridae. Not available as a family-group name: not based on a genus.

ADESMACEA Blainville, 1824
Reference: *Dictionnaire des Sciences Naturelles*, 32: 358

Remarks: Established as a family [containing the genera *Pholas*, *Teredina*, *Teredo*, *Fistulana* and *Septaria*] and not available as such (not based on a genus). Ranked by Dall (1896: 423) as superfamily. See also higher category list.

ADRANIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*, 80: 19, 25

Type genus: *Adrana* H. Adams & A. Adams, 1858

ADULINAE Scarlato & Starobogatov, 1979
Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24

Type genus: *Adula* H. Adams & A. Adams, 1857

AENIGMOCONCHIDAE Betekhtina, 1968
Reference: [in Betekhtina & Soukhov] *Akademiia Nauk SSSR, Sibirskoe Otdelnie, Institut Geologii i Geofiziki, Trudy*, 23: 37

Type genus: †*Aenigmoconcha* Benedictova, 1950

Remarks: Original spelling Aenigmoconchiidae.

AEQUIPECTININAE F. Nordsieck, 1969 [October]

Reference: *Die europäischen Meeresmuscheln (Bivalvia)*: 49

Type genus: *Aequipecten* P. Fischer, 1886

Remarks: -ini, Waller (1993: 198, 199).

AETHERIIDAE. See Etheriidae.

AFGHANODESMATIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 19, 25

Type genus: †*Afghanodesma* G. Termier & H. Termier, 1971

Remarks: -oidea, same reference.

AHTIOCONCHIDAE Eberzin, 1960

Reference: *Osnovy Paleontologii. Molljuskii. Pantsirnye, Dvustvorchatye, Lopatonogie*: 74

Type genus: †*Ahtioconcha* Öpik, 1930

ALASMIDONTINAE Rafinesque, 1820 [September]

Reference: *Annales Générales des Sciences Physiques* [Bruxelles], 5: 317

Type genus: *Alasmidonta* Say, 1818

Remarks: Original spelling Alasmidia. Also spelled Alasmodoninae and Alasmodontinae [based on *Alasmodon*, an unjustified emendation of *Alasmidonta*] by Swainson (1840: 268, 381). Precedence of simultaneously published Anodontinae determined by First Reviser action by Graf & Cummings (2006: 392).

ALATOCONCHIDAE H. Termier, G. Termier & de Lapparent, 1974

Reference: *Annales de la Société Géologique du Nord*, 93(1): 75

Type genus: †*Alatoconcha* H. Termier, G. Termier & de Lapparent, 1974

Remarks: -inae, Yancey & Ozaki (1986: 120).

ALLODESMATIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 537

Type genus: †*Allodesma* Ulrich, 1894

Remarks: Original spelling Allodesmidae.

ALLORISMATIDAE Beurlen, 1954 [19 December]

Reference: *Paleontologia do Parana*: 123

Type genus: †*Allorisma* King, 1844

Remarks: Original spelling Allorismidae. Independently declared new by Astafieva-Urbajtis

(1964: 205). -oidea [as Allerismatacea], Cox (1960: 85).

ALOIDIDAE Thiele, 1934

Reference: *Handbuch der systematischen Weichtierkunde*, 2: 925

Type genus: *Aloidis* Megerle von Mühlfeld, 1811

Remarks: Thiele treated “*Corbula* (Bruguière) Lamarck 1799 non Röding 1798” as a synonym of *Aloidis*, and he implicitly introduced Aloididae as a replacement name for Corbulidae. However, *Corbula* Bruguière, 1797, is a valid name, and Aloididae has not won general acceptance over Corbulidae.

ALULINAE N. J. Morris, Dickins & Astafieva-Urbajtis, 1991

Reference: *Bulletin of the British Museum (Natural History)*, Geology Series, 47(1): 94

Type genus: †*Alula* Girty, 1912

Remarks: Attributed in error by the authors to Mailleux, 1937.

ALVEINIDAE Glibert & van de Poel, 1966 [31 December]

Reference: *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique*, ser. 2, 82: 21

Type genus: †*Alveinus* Conrad, 1865

Remarks: Not available: no description.

AMBIGOSTREINI Malchus, 1990

Reference: *Berliner Geowissenschaftliche Abhandlungen*, ser. A, 125: 175

Type genus: †*Ambigostrea* Malchus, 1990

AMBLEMENAE Rafinesque, 1820 [September]

Reference: *Annales Générales des Sciences Physiques* [Bruxelles], 5: 310

Type genus: *Amblema* Rafinesque, 1820

Remarks: Original spelling (subfamily) Amblemidia. Independently declared new subfamily by Modell (1942: 180). -idae, Starobogatov (1970: 63); -ini, J. B. Burch (1975: 2).

AMBONYCHIIDAE S. A. Miller, 1877

Reference: *The American Palaeozoic fossils*: 180

Type genus: †*Ambonychia* Hall, 1847

Remarks: -inae, Tryon (1884: 274) / Hoernes (1884: 216); -oidea [as -acea], Newell (1965: 17).

AMERICUNIONINAE Guo, 1986

Reference: *Yunnan Geology*, 5(4): 342, 347

Type genus: †*Americunio* Guo, 1986

AMNIGENIIDAE Khalfin, 1948

Reference: *Izvestiia Tomskogo Politekhnicheskogo Instituta*, 65(1): 225

Type genus: †*Amnigenia* Hall, 1885

AMOTAPIDAE Olsson, 1928 [19 April]

Reference: *Bulletins of American Paleontology*, 14(52): 22 [68]

Type genus: †*Amotapus* Olsson, 1928

AMPHICOELIIDAE S. A. Miller, 1889 [after October]

Reference: *North American geology and paleontology*: 457

Type genus: †*Amphicoelia* Hall, 1867

AMPHIDESMATIDAE Latreille, 1825

Reference: *Familles naturelles du règne animal*: 221

Type genus: *Amphidesma* Lamarck, 1818

Remarks: Original spelling Amphidesmites (Latin), first used as a vernacular name, with the same spelling, by Latreille (1824: 333). Iredale (1915: 489) independently re-established Amphidesmatidae to replace Mesodesmatidae, because he considered *Mesodesma* Deshayes, 1832, a synonym of *Amphidesma*. See also Semelinae.

AMPHIDONTEINAE Vialov, 1983

Reference: *Doklady Akademii Nauk Ukrainskoi SSR*, ser. B, 11: 8

Type genus: †*Amphidonte* Fisher de Waldheim, 1829

AMPHIKOILINAE Novozhilov, 1953

Reference: *Trudy Akademii Nauk SSSR*, 92(4): 827

Type genus: †*Amphikoilum* Novozhilov, 1953

Remarks: Described as a crustacean, transferred to Mollusca by Pogorevich (1975).

AMUSIIDAE Ridewood, 1903 [31 January]

Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 196, 207

Type genus: *Amusium* Röding, 1798

Remarks: Original spelling Amussiidae, based on *Amussium* Herrmannsen, 1846, an unjustified emendation of *Amusium*. -inae, H. Watson (1930: 29). When he established Amusiidae, Ridewood used *Amusium* in the sense of *Propeamussium* [i.e. he used Amusiidae in the sense of Propeamussiidae], but the type species of *Amusium* belongs to the family Pectinidae. Under Art. 41, the case should be brought to the Commission for a ruling; however, Amusiidae / -inae is

not in current use, and stability is best maintained by including Amusiidae in the family Pectinidae.

AMUSSIOPECTININAE Glibert & van de Poel, 1965 [15 November]

Reference: *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique*, ser. 2, 78: 14

Type genus: †*Amussiopecten* Sacco, 1897

Remarks: Not available: no description.

ANADARINAE Reinhart, 1935 [August]

Reference: *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 11(13): 38

Type genus: *Anadara* Gray, 1847

Remarks: -idae, Scarlato & Starobogatov (1979a: 25).

ANATINELLIDAE Deshayes, 1853 [1 January]

Reference: [in Gray, ed.] *Annals and Magazine of Natural History*, ser. 2, 11(61): 43

Type genus: *Anatinella* G. B. Sowerby I, 1833

Remarks: Original spelling Anatinelladae. -inae, Dall (1895a: 556).

ANATINIDAE Gray, 1840 [16 October]

Reference: *Synopsis of the contents of the British Museum*, ed. 42: 135, 150

Type genus: *Anatina* Lamarck, 1818

Remarks: Invalid: Type genus a junior homonym of *Anatina* Schumacher, 1817 [Mactridae]. -inae [as Anatinana], Bronn (1862: 476, 502); -oidea [as -acea], Dall (1896: 387). See Laternulidae.

ANDITRIGONIIDAE H. A. Leanza, 1993 [20 October]

Reference: *Bulletins of American Paleontology*, 105(343): 45

Type genus: †*Anditrigonia* Levy, 1967

ANNULICONCHINAE Astafieva, 1995 [before July]

Reference: *Paleontologicheskii Zhurnal*, 1995(2): 32, 33

Type genus: †*Annuliconcha* Newell, 1938

Remarks: -idae [declared new], Newell & Boyd (1995 [13 December]: 57).

ANODONTINAE Rafinesque, 1820 [September]

Reference: *Annales Générales des Sciences Physiques* [Bruxelles], 5: 316

Type genus: *Anodonta* Lamarck, 1799

Remarks: Original spelling Anodontidia. Spelling Anodoninae [based on the unjustified emendation *Anodon* Swainson, 1840] also

used by Swainson (1840: 268). Precedence of simultaneously published Unioninae determined by First Reviser action by Morrison (1956: 16); precedence over simultaneously published Alasmidontinae determined by First Reviser action by Graf & Cummings (2006: 392). -idae, Phillips (1855: 221); -ini, J. B. Burch (1975: 2).

ANODONTITINAE Modell, 1942 [15 October]
Reference: *Archiv für Molluskenkunde*, 74(5–6): 175

Type genus: *Anodontites* Bruguière, 1792
Remarks: Precedence over simultaneously published Glabarinae determined by First Reviser action by Parodiz & Bonetto (1963: 206).

ANODONTOPSIDAE S. A. Miller, 1889 [after October]

Reference: *North American geology and palaeontology*: 457

Type genus: †*Anodontopsis* M'Coy, 1851

ANOMIINAE Rafinesque, 1815

Reference: *Analyse de la nature*: 148

Type genus: *Anomia* Linnaeus, 1758

Remarks: Original spelling (subfamily) Anomia. First introduced as the vernacular “les anomiés” by Blainville (1814: 179). -idae [as Anomiadae], Gray (1840b: 142, 151); -oidea [as -acea], Gill (1871: 22).

ANOMOPTYCHIDAE H. A. Vokes, 1967 [16 June]

Reference: *Bulletins of American Paleontology*, 51(232): 235

Type genus: †*Anomoptychus* Douvillé, 1906

Remarks: Introduced, in violation of Art. 40.1, as a replacement name for Trechmanellidae, based on *Trechmanella*, which Vokes considered to be a synonym of *Anomoptychus*.

ANOPAEINAE Tsagareli & Gambashidze, 1984

Reference: *Paleontologicheskij Sbornik* [Lwow], 21: 52

Type genus: †*Anopaea* Eichwald, 1861

Remarks: Original spelling Anopeinae. Not available: no description.

ANTACTINODIONTIDAE Guo, 1980 [January]

Reference: *Acta Palaeontologica Sinica*, 19(1): 51

Type genus: †*Antactinodion* Guo, 1980

Remarks: Family and genus independently declared new by Guo (1982: 38). -oidea, Nevesskaja (2003: 618).

ANTHRACONAUTIDAE Kanev, 1980

Reference: *Akademiia Nauk SSSR, Komi Filial, Trudy Instituta Geologii*, 33: 45

Type genus: †*Anthraconauta* Pruvost, 1930

Remarks: Not available: no description. Name attributed by Kanev to Papin, without date or reference. Name not located in any of Papin's works.

ANTHRACOSIIDAE Amalitsky, 1892 [November]

Reference: *Palaeontographica*, 39(4–6): 196

Type genus: †*Anthracosia* King, 1856

Remarks: Original spelling Anthracosidae. -inae, same reference; -oidea [as -acea], Newell (1965: 18). See also Carbonicolidae.

ANTILLOCAPRININAE MacGillavry, 1937

Reference: *Geographische en Geologische Mededelingen, Physiographisch-Geologische series*, 14: 46, 106

Type genus: †*Antillocaprina* Trechmann, 1924

Remarks: -idae, Skelton (1978: 317).

ANTIPLEURINAE Conrath, 1887 [14 July]

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 96(1): 49

Type genus: †*Antipleura* Barrande, 1881

Remarks: -idae, Grobben (1892a: 142; 1892b: 373); -oidea, Scarlato & Starobogatov (1979a: 20).

APIOTRIGONIINAE Tashiro, 1979 [30 December]

Reference: *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 116: 181

Type genus: †*Apiotrigonia* Cox, 1952

ARCHAEOCARDIIDAE Khalfin, 1940

Reference: *Trudy nauchnoi konferentsii po izucheniiu i osvoeniiu proizvoditelnykh sil Sibiri*, 2: 264

Type genus: †*Archaeocardium* Khalfin, 1940

Remarks: Available under Art. 13.5 (combined description of family and genus): no separate description for family, but family monogeneric, based on *Archaeocardium*, which is diagnosed. Independently declared new by Khalfin (1948: 443).

ARCHANODONTIDAE Modell, 1957 [28 December]

Reference: *Archiv für Molluskenkunde*, 86(4–6): 184

Type genus: †*Archanodon* Howse, 1878
 Remarks: -oidea [as -acea; declared new], Weir ([in Moore, ed.] 1969: 402, 404).

ARCICARDIINI Nevesskaja, 1986
 Reference: [in Nevesskaja et al.] *Trudy Paleontologicheskogo Instituta*, 220: 190
 Type genus: †*Arcicardium* P. Fischer, 1887

ARCIDAE Lamarck, 1809
 Reference: *Philosophie zoologique*: 318
 Type genus: *Arca* Linnaeus, 1758
 Remarks: Original spelling "Les arcacées" (vernacular). First latinized, as Arcaceae, by Goldfuss (1820: 609). Name attributed to Lamarck, 1809, by Newell ([in Moore, ed.] 1969: 250). -inae, Gray (1854a: 417); -oidea [as -acea], Gill (1871: 21).

ARCIDOPSINAE Starobogatov, 1970
 Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinentalnykh vodoemov zemnogo shara*: 61, 283
 Type genus: *Arcidopsis* Simpson, 1900

ARCINELLIDAE Scarlato & Starobogatov, 1971
 Reference: [in Nevesskaja et al.] *Paleontologicheskii Zhurnal*, 1971(2): 17
 Type genus: *Arcinella* Schumacher, 1817
 Remarks: -oidea, same reference.

ARCOMYIDAE P. Fischer, 1887 [15 June]
 Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (11): 1165
 Type genus: †*Arcomya* Roemer, 1839

ARCOPAGIINAE Kuroda, Habe & Oyama, 1971 [27 September]
 Reference: *The sea shells of Sagami Bay*: 449 [English text only]
 Type genus: *Arcopagia* T. Brown, 1827
 Remarks: Not available: no description.

ARCTICIDAE Newton, 1891 [22 August] (1844)
 Reference: *Systematic list of the F. E. Edwards collection of British Oligocene and Eocene Mollusca in the British Museum (Natural History)*: 295
 Type genus: *Arctica* Schumacher, 1817
 Remarks: Established as a substitute name for Cyprinidae d'Orbigny, 1844, considered invalid by Newton because its type genus *Cyprina* Lamarck, 1818, was believed by him to be a junior homonym of "Cyprina Linnaeus, 1766" [in fact *Cyprinus* Linnaeus, 1758 (Pisces)]. A bivalve family name based

on *Cyprina* would be nomenclaturally valid; however Arctidae is in prevailing usage, and it is conserved under Art. 40.2 with the priority of Cyprinidae (1844). See also Cypriniadeidae. -oidea [as -acea, in synonymy of Trapeziacea], Habe (1953: 285).

ARCTOSTREINAE Vialov, 1983
 Reference: *Doklady Akademii Nauk Ukrainskoi SSR*, ser. B, 11: 7
 Type genus: †*Arctostrea* Pervinquière, 1910
 Remarks: -idae, Carter, herein.

ARCUATULINAE Scarlato & Starobogatov, 1979
 Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24
 Type genus: *Arcuatula* Jousseume [in Lamy], 1919

ARCULLAEINAE Newell, 1969
 Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 268
 Type genus: †*Arcullaea* H. A. Vokes, 1946

ARHOURIELLIDAE Geyer & Streng, 1998 [December]
 Reference: *Revista Espanola de Paleontologia, Numero extra, Homenaje al Prof. G. Vidal*: 93
 Type genus: †*Arhouriella* Geyer & Streng, 1998
 Remarks: According to Carter et al. (2000: 49), the holotype of *Arhouriella opheodontoides* Geyer & Streng, 1998, the type species of the genus, is probably an ostracode; the paratype may be a member of the Bivalvia, but it is not obviously the same taxon as the holotype.

ARTEMINAE Hutton, 1880
 Reference: *Manual of the New Zealand Mollusca*: 149
 Type genus: *Artemis* Poli, 1791
 Remarks: *Artemis* is an incorrect subsequent spelling of *Arthemis* Poli, 1791. However, *Artemis* was the spelling in prevailing usage when Hutton established Arteminae, until *Artemis* was permanently displaced by its senior synonym *Dosinia* Scopoli, 1777.

ASAPHIDAE Winckworth, 1932 [June]
 Reference: *Journal of Conchology*, 19(7): 245
 Type genus: *Asaphis* Modeer, 1793
 Remarks: Name only. First diagnosed and -inae [declared new], Glibert & van de Poel (1967: 119). Homonym of Asaphidae Burmeister, 1843, based on *Asaphus* Brongniart in Brongniart & Desmarest, 1822 [Arthropoda].

ASIPHONIDAE Choffat, 1886

Reference: *Recueil d'études paléontologiques sur la faune crétacique du Portugal*, 1: 34, pl. 1

Remarks: Division of bivalves (see also Asiphonia in higher category list). Not available: not based on a genus.

ASOELLIDAE Begg & H. J. Campbell, 1986 [5 March]

Reference: *New Zealand Journal of Geology and Geophysics*, 28(4): 727

Type genus: †*Asoella* Tokuyama, 1959

Remarks: -inae / -ini, Waterhouse (2001: 124, 125).

ASPATHARIINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 177

Type genus: *Aspatharia* Bourguignat, 1885

Remarks: Precedence over simultaneously published Spathopsinae determined by First Reviser action by Graf & Cummings (2006: 394).

ASPERGILLIDAE Burmeister, 1837

Reference: *Handbuch der Naturgeschichte*, 2: 490

Type genus: *Aspergillum* Lamarck, 1818

Remarks: Original spelling (family) Aspergillina. -inae, Tryon (1884: 117). Under Art. 23.9 of the Code, Aspergillidae Burmeister, 1837, is here declared a nomen oblitum and Clavagellidae d'Orbigny, 1844, a nomen protectum: see under Clavagellidae.

ASTARTELLINAE Boyd & Newell, 1968

Reference: *American Museum Novitates*, 2328: 23, 45

Type genus: †*Astartella* Hall, 1858

ASTARTIDAE d'Orbigny, 1844 (1840)

Reference: *Paléontologie française. Terrains crétacés*, 3: 51

Type genus: *Astarte* J. Sowerby, 1816

Remarks: When he established Astartidae, d'Orbigny did not cite Crassinidae, but treated *Crassina* Lamarck, 1818, as a synonym of *Astarte*. Astartidae is in prevailing usage and is conserved under Art. 40.2 with the priority of Crassinidae (1840). -inae [as -ana], Bronn (1862: 475, 500); -oidea [as -acea], Dall (1895a: 538).

ASTARTILINAE Waterhouse, 1969 [August]

Reference: *New Zealand Geological Survey Paleontological Bulletin*, 41: 55

Type genus: †*Astartila* Dana, 1847

ASTHENOTHAERINAE P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (11): 1168

Type genus: *Asthenothaerus* P. P. Carpenter, 1864

ATOMODESMATINAE Waterhouse, 1976 [August]

Reference: *Journal of the Royal Society of New Zealand*, 6(2): 248

Type genus: †*Atomodesma* Beyrich, 1865

Remarks: Original spelling Atomodesminae. -idae, Astafieva (1993: 58).

ATRETIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 21

Type genus: †*Atreta* Etallon, 1862

AUCELLINAE P. Fischer, 1886 [30 April]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (10): 950

Type genus: †*Aucella* Keyserling, 1846

Remarks: -idae, Lahusen (1897: 351). Invalid: Placed on the Official Index by Opinion 492, but attributed in error to Lahusen, 1897. See Buchiidae.

AUCELLININI Waterhouse, 2001 [1 July]

Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 125

Type genus: †*Aucellina* Pompeckj, 1901

Remarks: -inae, Waterhouse (2008: 170).

AULACOMYELLINAE Ichikawa, 1958 [October]

Reference: *Palaeontographica*, ser. A, 111(5–6): 186, 189, 197

Type genus: †*Aulacomyella* Furlani, 1910

Remarks: -idae, Romanov (1984: 84); -oidea, Waterhouse (2008: 171).

AUPOURIIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 23

Type genus: *Aupouria* Powell, 1937

Remarks: Original spelling Auporiidae, based on *Auporia*, an incorrect subsequent spelling of *Aupouria*. Independently declared new by Scarlato & Starobogatov (1979a: 21, 30).

AUSTROCHLAMYDINI Jonkers, 2003

Reference: *Monographs of Marine Mollusca*, 5: 59

Type genus: *Austrochlamys* Jonkers, 2003

AUSTROTRIGONIINAE Skwarko, 1968

Reference: *Commonwealth of Australia, Department of National Development, Bureau of*

Mineral Resources, Geology and Geophysics, Bulletin 80: 176

Type genus: †*Austrotrigonia* Skwarko, 1963

AVICARDIINI Popov, 1977

Reference: [in Kafanov & Popov] *Paleontologicheskii Zhurnal*, 1977(3): 63

Type genus: †*Avicardium* Kolesnikov, 1950

AVICULARIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 23, 35

Type genus: †*Avicularium* Gray, 1853

AVICULIDAE G. A. Goldfuss, 1820

Reference: *Handbuch der Zoologie*, Abt. 1: xlii, 607

Type genus: *Avicula* Bruguière, 1792

Remarks: Original spelling (family) Aviculae. -inae [as "Trib. Aviculidae", below family Mytilacea], Mörch (1853: 50); -oidea [as -acea], Gill (1871: 21). See Pteriidae.

AVICULOCARDIINI Paramonova, 2001

Reference: [in Nevesskaja, Paramonova & Popov] *Paleontological Journal*, 35, supplementary issue 3: 149, 181

Type genus: †*Aviculocardium* Bagdasarian, 1978

Remarks: -ina, Bieler, Carter & Coan, herein.

AVICULOPECTININAE Meek & Hayden, 1865 [April]

Reference: *Smithsonian Contributions to Knowledge*, 14(172): 49

Type genus: †*Aviculopecten* M'Coy, 1851

Remarks: Original spelling Aviculo-pectininae. -idae, S. A. Miller (1889: 458); -oidea, Nevesskaja et al. (1971: 15).

AXINAEINAE H. Adams & A. Adams, 1858 [January]

Reference: *The Genera of Recent Mollusca*, 2: 541

Type genus: *Axinaea* Poli, 1791

AXINOPSIDINAE F. R. Bernard, 1983 [about 15 April]

Reference: *Canadian Special Publication of Fisheries and Aquatic Sciences*, 61: 29, 68

Type genus: *Axinopsida* Keen & Chavan, 1951

AZORIDAE Leach, 1852

Reference: *A synopsis of the Mollusca of Great Britain*: 248, 252

Type genus: *Azor* [see Remarks]

Remarks: When he established Azoridae, Gray used *Azor* in the sense that Leach in his MS had originally intended to use it, i.e. for what is now *Azorinus* Récluz, 1869 [family Solecurtidae]. However, in the meantime, J. De C. Sowerby (1824) had made Leach's MS name available, but with a different meaning, selecting an Eocene species of Psammobiidae as type species. Under Art. 41, the case should be brought to the Commission; however, the name Azoridae is not currently in use, and will end up either a synonym of Solecurtidae d'Orbigny, 1846, or of Psammobiidae Fleming, 1828.

BABINKIDAE Horný, 1960

Reference: *Vestník Ustředního Ústavu Geologického*, 35(6): 480

Type genus: †*Babinka* Barrande, 1881

Remarks: -oidea [as -acea], McAlester (1966: 438).

BAIDIOSTRACIDAE Fang & Cope, 2008 [September]

Reference: *Alcheringa*, 32(3): 306

Type genus: †*Baidiostraca* Guo, 1988

BAKEVELLIIDAE King, 1850

Reference: *A monograph of the Permian fossils of England*: 166

Type genus: †*Bakevella* King, 1848

Remarks: -inae, Eberzin (1960: 79); -oidea, Nevesskaja et al. (1971: 15).

BANKIINAE Turner, 1966

Reference: *A survey and illustrated catalogue of the Teredinidae*: 57

Type genus: *Bankia* Gray, 1842

BARBATIIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25

Type genus: *Barbatia* Gray, 1842

Remarks: -inae, same reference.

BARRETTIINAE Chubb, 1971 [17 September]

Reference: *Palaeontographica Americana*, 7(45): 207

Type genus: †*Barrettia* S. P. Woodward, 1862

BARTLETTIINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 176

Type genus: *Bartlettia* H. Adams, 1867

BASTEROTIIDAE Cossmann, 1909

Reference: [in Cossmann & Peyrot] *Actes de la Société Linnéenne de Bordeaux*, 63(3): 205

Type genus: †*Basterotia* M. Hörnes, 1859

BATHMOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 16

Type genus: †*Bathmoceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

BATHYARCIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24

Type genus: *Bathyarca* Kobelt, 1891

Remarks: -oidea, same reference.

BATHYMODIOLINAE Kenk & Wilson, 1985 [9 July]

Reference: *Malacologia*, 26(1–2): 255

Type genus: *Bathymodiolus* Kenk & Wilson, 1985

BATHYSPINULINAE Coan & Scott, 1997

Reference: *Santa Barbara Museum of Natural History, Contributions in Science*, 1: 2, 22

Type genus: *Bathyspinula* Allen & Sanders, 1982

Remarks: Nom. nov. pro Spinulinae Allen & Sanders, 1982, invalid because its type genus is a junior homonym. Coan & Scott considered in error that Bathyspinulinae has the priority of Spinulinae, but *Bathyspinula* is not a synonym of, or a replacement name for *Spinula*, and thus Art. 40.2 does not apply. -idae, La Perna (2008: 156).

BATOLITIDAE Yanin, 1990

Reference: [in Menner ed.] *Sistematika, filogeniia bespozvonochnykh. Kriterii vyschikh taksonov*: 67

Type genus: †*Batolites* Montfort, 1808

BAYLEIIDAE Munier-Chalmas, 1873 [31 January]

Reference: *Journal de Conchyliologie*, 21(1): 73

Type genus: †*Bayleia* Munier-Chalmas, 1873

Remarks: Original spelling Bayleidae. Rejected under Art. 23b of the first edition of the Code as a *nomen oblitum* by Deschaseaux & Perkins (in Moore, ed., 1969: 779); under Art. 23.12 of the current edition, Bayleidae must not be given precedence over Requiieniidae, currently regarded as its junior synonym.

BEICHUANIIDAE Liu & Gu, 1988 [June]

Reference: [in Liu] *Devonian stratigraphy, paleontology and sedimentary facies of Longmenshan, Sichuan*: 259 [Chinese text], 401 [English text]

Type genus: †*Beichuania* Liu & Gu, 1988

Remarks: -oidea [as -acea], same reference. Independently declared new by Gu & Liu (1988 [December]: 359).

BELOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 22

Type genus: †*Beloceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

BENTHOCARDIELLIDAE Iredale & McMichael, 1962 [30 May]

Reference: *The Australian Museum, Sydney, Memoir* 11: 18

Type genus: *Benthocardiella* Powell, 1930

Remarks: Not available: name only, no description.

BERNARDINIDAE Keen, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 650

Type genus: *Bernardina* Dall, 1910

Remarks: Not available (name only, no description) from Keen (1963: 91).

BINIPECTINIDAE Feng & Liu, 1990

Reference: *Earth Science, Journal of China University of Geosciences*, 15(2): 128 [Chinese], 130 [English abstract]

Type genus: †*Binipecten* Feng & Liu, 1990

BIRADIOLITINAE Dechaseaux & Coogan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 810

Type genus: †*Biradiolites* d'Orbigny, 1850

Remarks: Not available (vernacular name introduced after 1900) from "Biradiolitinés" of Douvillé (1903: 473).

BOEHMICERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 18

Type genus: †*Boehmiceramus* Heinz, 1932

Remarks: Not available: type genus not an available name under Art. 13.1.1 (no description).

BORNIINAE F. R. Bernard, 1983 [about 15 April]

Reference: *Canadian Special Publication of Fisheries and Aquatic Sciences*, 61: 31, 68

Type genus: *Bornia* Philippi, 1836

BORNIOLIDAE Iredale & McMichael, 1962 [30 May]

Reference: *The Australian Museum, Sydney, Memoir* 11: 20

Type genus: *Borniola* Iredale, 1924

Remarks: Not available: name only, no description. Not available from Ponder (1971: 137, 139; no description and not used as a valid name); nor from Habe (1977: 141; not used as a valid name); nor from Habe (1981: 98; no description); nor from Vaught (1989: 126, as -inae, in the synonymy of Borniinae); nor from Higo, Callomon & Goto (1999: B6951).

BOSITRIDAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 174

Type genus: †*Bositra* de Gregorio, 1886

BOTULINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24

Type genus: *Botula* Mörch, 1853

Remarks: *Botula* Mörch is not made invalid by “*Botula* Leske, 1776” [Echinodermata], which is an erroneous entry in *Nomenclator Zoologicus* for *Rotula*; see Winckworth (1943: 187).

BRACHIDONTINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24

Type genus: *Brachidontes* Swainson, 1840

Remarks: Original spelling Brachiodontinae, based on *Brachiodontes*, an incorrect subsequent spelling of *Brachidontes*.

BRACHYANODONTINI Bogatov, Sayenko & Starobogatov, 2002

Reference: *Zoologicheskii Zhurnal*, 81(5): 521, 527, 528

Type genus: *Brachyanodon* Crosse & P. Fischer, 1894

Remarks: Name attributed by the authors to “Crosse & Fischer 1893” who, however, established the genus, but no family-group name based on that genus. Not available: not explicitly indicated as an intentionally new name (Art. 16.1) and type genus not cited (Art. 16.2). For the same reasons, not made available by Starobogatov et al. (2004: 30).

BRANSONIIDAE Pojeta & Runnegar, 1976

Reference: *United States Geological Survey Professional Paper*, 968: 71

Type genus: †*Bransonia* Pojeta & Runnegar, 1976

Remarks: Established as a family of Rostroconchia. Classified in the bivalve superorder Septibranchia by Starobogatov (1977), an opinion not followed by later authors.

BRAZZAEINAE Leloup, 1950 [31 December]

Reference: *Exploration hydrobiologique du Lac Tanganika (1946–1947). Résultats Scientifiques*, 3(1): 7, 73, 79

Type genus: *Brazzaea* Bourguignat, 1885

Remarks: Original spelling Brazzaeainae. Leloup did not explicitly diagnose the subfamily, but he established it as a monotypic subfamily based on *Brazzaea*, which he differentially diagnosed from Unionidae and Mutelidae. We regard this as satisfying the criteria of availability under Art. 13.1.1.

BRECHITINAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologica Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b, 28

Type genus: *Brechites* Guettard, 1770

BRYOPINAE Tryon, 1862 [before 31 March]

Reference: *Proceedings of the Academy of Natural Sciences of Philadelphia*, 13: 472

Type genus: *Bryopa* Gray, 1847

BUCARDIIDAE H. Adams & A. Adams, 1857 [April]

Reference: *The Genera of Recent Mollusca*, 2: 460

Type genus: *Bucardia* Schumacher, 1817

Remarks: When they established Bucardiidae, H. & A. Adams did not cite Glossidae or Isocardiidae, but treated *Glossus* and *Isocardia* as synonyms of *Bucardia* [which they attributed to Lister]. Bucardiidae is not in prevailing usage, and Art. 40.2 does not apply.

BUCHIIDAE Cox, 1953 (1886)

Reference: *Falkland Islands Dependencies Survey, Scientific Reports*, 4: 6

Type genus: †*Buchia* Roullier, 1845

Remarks: Replacement name for Aucellidae, based on *Aucella* Keyserling, 1846, a junior synonym of *Buchia*. Buchiidae is in prevailing usage and is conserved under Art. 40.2, with the priority of Aucellinae (1886). Placed on the Official List by Opinion 492 (1957: 212). -oidea, Nevesskaja et al. (1971: 15).

BUCHIOLINAE Grimm, 1998 [June]

Reference: *Mémoires Suisses de Paléontologie*, 118: 46

Type genus: †*Buchiola* Barrande, 1881

Remarks: -idae, Kříž (2004: 89).

BUCHOTRIGONIINAE H. A. Leanza, 1993 [20 October]

Reference: *Bulletins of American Paleontology*, 105(343): 56

Type genus: †*Buchotrigonia* Dietrich, 1938

Remarks: -idae, Pérez & Reyes (1997: 247).

BURMESIIDAE Healey, 1908

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica*, new ser., 2(4): 56

Type genus: †*Burmesia* Healey, 1908

BUTOVICELLIDAE Kříž, 1965

Reference: *Vestník Ustředního Ústavu Geologického*, 40(3): 207

Type genus: †*Butovicella* Kříž, 1965

BYSSIFERIA Lamarck, 1809

Reference: *Philosophie zoologique*, 1: 317

Remarks: Original spelling “Les byssifères” (vernacular). Latinized by Rafinesque (1815: 147). Established as a family containing the genera “Houlette”, “lime”, “pinne”, “moule”, “modiole(?)” and “crénatule”, and not available as such (not based on a genus).

CADOMIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 19, 25

Type genus: †*Cadomia* Tromelin, 1877

CAELATURINAE. See Coelaturinae.**CAELONOTIDAE** M'Coy, 1855

Reference: [in Sedgwick] *A synopsis of the classification of the British Palaeozoic rocks*: 275

Remarks: Includes *Sanguinolites*, *Grammysia*, *Leptodomus*, and *Myoconcha*. Spelled Coelotonotidae by Hind (1900 [in 1896–1901]: 361). Not available: not based on a genus.

CAESTOCORBULINAE H. A. Vokes, 1945 [10 October]

Reference: *Bulletin of the American Museum of Natural History*, 86: 6, 20

Type genus: †*Caestocorbula* E. Vincent, 1910

CAFFERIINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 188

Type genus: *Cafferia* Simpson, 1900

Remarks: -ini, Starobogatov (1970: 66).

CALCICANICULARIINI Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 131

Type genus: †*Calcicanicularia* Waterhouse, 1983

CALLISTINAE Habe & Kosuge, 1967

Reference: *Kai [Hyojun genshoku zukan zenshu]*, 3]: 150

Type genus: *Callista* Poli, 1791

Remarks: Independently declared nov. subfam. by F. Nordsieck (1969: 108). Homonym of Callistidae Laporte de Castelnau, 1834, based on *Callistus* Bonelli, 1810 [Coleoptera].

CALLOARCINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25

Type genus: *Calloarca* Gray, 1857

CALLOCARDIIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 551

Type genus: *Callocardia* A. Adams, 1864

CALVAENTOLIINAE Kasum-Zade, 2003

Reference: [Advance in research of Mesozoic bivalve mollusks in Azerbaijan Order Pectinoida: revision and systematics]: 44, 82

Type genus: †*Calvaentolium* Romanov, 1985

CAMPTONECTINAE Habe, 1977

Reference: *Systematics of Mollusca in Japan (Bivalvia and Scaphopoda)*: 87

Type genus: †*Camptonectes* Agassiz, 1864

Remarks: Established independently by Kanjilal (1979: 117) and again by Kasum-Zade (2003: 49, 83, as Camptonectesinae). -idae [declared new], Dickan (1991: 7).

CAMYIDAE Hinz-Schallreuter, 2000 [August]

Reference: *Revista Espanola de Micropaleontologia*, 32(2): 234

Type genus: †*Camya* Hinz-Schallreuter, 1995

CAPRINELLIDAE Gill, 1871 [February]

Reference: *Smithsonian Miscellaneous Collections*, 227: 22

Type genus: †*Caprinella* d'Orbigny, 1847

Remarks: see under Ichthyosarcolitini.

CAPRINIDAE d'Orbigny, 1847

Reference: *Comptes Rendus Hebdomadaires de l'Académie des Sciences*, 25: 269

Type genus: †*Caprina* d'Orbigny, 1822

Remarks: Erected as the vernacular “Caprinidées” by d’Orbigny (1842: 176), which is not considered an available name by Mancenido, Owen & Morris (1993: 198). -inae, MacGillavry (1937: 144); -oidea, Yanin (1990: 66). Priority of simultaneously published Radiolitidae determined by First Reviser action by Bouchet & Rocroi, herein.

CAPRINULIDAE Yanin, 1990

Reference: [in Menner ed.] *Sistematika, filogeniia bespozvonochnykh. Kriterii vydeleniia vyschikh taksonov*: 66

Type genus: †*Caprinula* d’Orbigny, 1847

CAPRINULOIDEINAE Damestoy, 1971 [30 July]

Reference: *Bulletin du Muséum National d’Histoire Naturelle*, ser. 2, 42(5): 1005, 1006

Type genus: †*Caprinuloidea* Palmer, 1928

Remarks: Original spelling Caprinuloidinae. Not available (no description) from MacGillavry (1970: 66, 73).

CAPROTINIDAE Gray, 1848 [1 December]

Reference: *Annals and Magazine of Natural History*, ser. 2, 2(12): 440

Type genus: †*Caprotina* d’Orbigny, 1842

Remarks: Original spelling Caprotinadae. -oidea, Nevesskaja et al. (1971: 17).

CAPSINAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b, 120

Type genus: *Capsa* Bruguière, 1797

CARBONICOLIDAE Cox, 1932 [25 November]

Reference: *The Quarterly Journal of the Geological Society of London*, 88(4): 625

Type genus: †*Carbonicola* M’Coy, 1855

Remarks: Introduced as a substitute name for Anthracosiidae, based on *Anthracosia*, by Cox considered a synonym of *Carbonicola*. However, *Carbonicola* and *Anthracosia* are not currently regarded as synonyms (see Classification), and Carbonicolidae must be evaluated on its own standing. Name only, no description in Cox, but used as valid before 2000, e.g., by Weir (1938: 12). -inae, Modell (1964: 79).

CARDIIDAE Lamarck, 1809

Reference: *Philosophie zoologique*, 1: 318

Type genus: *Cardium* Linnaeus, 1758

Remarks: Original spelling “Les cardiadées” (vernacular). First latinized [as Cardiaceae

“Cuv.”] by Schweigger (1820: 702. Attributed to Lamarck, 1809, in the Treatise. The spelling Cordiidae [Gistel, 1848: 172, as Cordiacea] is based on *Cordium* Gistel, 1848, an unjustified emendation of *Cardium*. -oidea [as -acea], Gill (1871: 19); -inae [as -ana], Bronn (1862: 475, 500); -ini, Kafanov & Popov (1977: 59).

CARDILIIDAE P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (11): 1120

Type genus: *Cardilia* Deshayes, 1835

Remarks: Independently declared new by Dall (1896: 421).

CARDINIIDAE Zittel, 1881

Reference: *Handbuch der Palaeontologie*, Abt. 1, Palaeozoologie, Bd. 2: 61

Type genus: †*Cardinia* Agassiz, 1841

Remarks: -oidea [as -acea], Tryon (1884: 235).

CARDIOLARIIDAE Cope, 1897 [August]

Reference: *Palaeontology*, 40(3): 736

Type genus: †*Cardiolaria* Munier-Chalmas, 1876

Remarks: -oidea, Cope (in Harper, Taylor & Crame, eds., 2000: 88).

CARDIOLIDAE R. Hoernes, 1884

Reference: *Elemente der Palaeontologie (Palaeozoologie)*: 222

Type genus: †*Cardiola* Broderip, 1839

Remarks: -oidea [as -acea], Cox (1960: 85); -inae, Newell & LaRocque (in Moore, ed., 1969: 245).

CARDIOMORPHIDAE S. A. Miller, 1877

Reference: *The American Palaeozoic fossils*: 180

Type genus: †*Cardiomorpha* de Koninck, 1841

CARDIOMYIDAE Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 13

Type genus: *Cardiomya* A. Adams, 1864

CARDITAMERINAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 548

Type genus: †*Carditamera* Conrad, 1838

CARDITELLIDAE Kuroda, Habe & Oyama, 1971 [27 September]

Reference: *The sea shells of Sagami Bay*: 603 [Japanese text], 387 [English text]

Type genus: *Carditella* E. A. Smith, 1881

Remarks: Not available (no description) from Iredale & McMichael (1962: 17). -inae, Habe (1977: 159).

CARDITESINAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 556

Type genus: *Cardites* Link, 1807

CARDITIDAE Férussac, 1822 [13 April]

Reference: *Tableaux systématiques des animaux mollusques*, 1: xlij

Type genus: *Cardita* Bruguière, 1792

Remarks: Original spelling "Les Cardites" (vernacular); first latinized [as Carditadæ] by Fleming (1828: 408, 417), and [as Carditaceæ] by Menke (1828: 64). -oidea [as -acea], Gill (1871: 20); -inae, Tryon (1884: 231).

CARYDIIDAE Haffer, 1959 [May]

Reference: *Palaeontographica*, ser. A, 112(5–6): 138

Type genus: †*Carydium* Beushausen, 1895

Remarks: -oidea, Nevesskaja et al. (1971: 13).

CARYOCORBULINAE H. A. Vokes, 1945 [10 October]

Reference: *Bulletin of the American Museum of Natural History*, 86: 5, 11

Type genus: †*Caryocorbula* J. A. Gardner, 1926

CASSIANELLIDAE Ichikawa, 1958 [October]

Reference: *Palaeontographica*, ser. A, 111(5–6): 195

Type genus: †*Cassianella* Beyrich, 1862

CASSIANOIDIDAE Newell & Boyd, 1995 [13 December]

Reference: *Bulletin of the American Museum of Natural History*, 227: 32

Type genus: †*Cassianoides* Newell & Boyd, 1995

Remarks: -ini, Waterhouse (2001: 121); -inae, Waterhouse (2008: 151).

CASTALIINAE Morretes, 1949

Reference: *Arquivos do Museu Paranaense*, 7: 21

Type genus: *Castalia* Lamarck, 1819

Remarks: Name only, no description. Available through its use as a valid name, e.g. by Parodiz & Bonetto (1963: 201, 204, as -ini).

CATAMARCAIIDAE Cope, 2000 [12 December]

Reference: [in Harper, Taylor & Crame, eds.] *The evolutionary biology of the Bivalvia*: 92

Type genus: †*Catamarcaia* Sánchez & Babin, 1993

Remarks: Original spelling Catamarcaidae.

CATELLIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 22

Type genus: †*Catella* Healey, 1908

CERASTODERMATINAE F. Nordsieck, 1969 [October]

Reference: *Die europäischen Meeresmuscheln (Bivalvia)*: 98

Type genus: *Cerastoderma* Poli, 1795

Remarks: -ini, Kafanov & Popov (1977: 60).

CERATOMYIDAE Arkell, 1934 [January]

Reference: *A monograph of British Corallian Lamellibranchia*, part 6: 315

Type genus: †*Ceratomya* Sandberger, 1864

Remarks: Name attributed by Arkell to Fischer, but P. Fischer (1887: 1164) used Ceromyidae (see that name). Spelling Ceratomyacidae used by Cox (1935: 186). Placed on the Official List by Opinion 742 (1965: 176). -oidea [as -acea], Runnegar (1974: 925, 933).

CERATOMYOPSIDAE Cox, 1964 [April]

Reference: *Proceedings of the Malacological Society of London*, 36(1): 40

Type genus: †*Ceratomyopsis* Cossmann, 1915

CERATOSTREONINAE Vialov, 1983

Reference: *Doklady Akademii Nauk Ukrain-skoi SSR*, ser. B, 11: 8

Type genus: †*Ceratostreon* Bayle, 1878

CERCOMYIDAE Crickmay, 1936 [30 April]

Reference: *Bulletin of the Geological Society of America*, 47(4): 558

Type genus: †*Cercomya* Agassiz, 1843

Remarks: Original spelling Cercomyacidae. Name only, no description. Available through its use as a valid name, e.g. by Scarlato & Starobogatov (1979a: 21, as -idae and -oidea; attributed to Crickmay).

CEROMYIDAE Récluz, 1869

Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): unnumbered table between pp. 34 and 35

Type genus: †*Ceromya* Agassiz, 1842

Remarks: Original spelling Ceromidae. Invalid: type genus a junior homonym of *Ceromya* Robineau-Desvoidy [Diptera]. Placed on the Official Index by Opinion 742 (1965: 176), but attributed in error to P. Fischer (1887: 1164). See Ceratomyidae.

CETOCONCHIDAE Ridewood, 1903 [31 January]
Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 187, 275
Type genus: *Cetoconcha* Dall, 1886

CETOMYINAE Krylova, 1997 [December]
Reference: *Ruthenica*, 7(2): 143, 144
Type genus: *Cetomya* Dall, 1889

CHAENINAE Gray, 1858b [9 November]
Reference: *Proceedings of the Zoological Society of London*, 26: 315
Type genus: *Chaena* Philipson, 1788
Remarks: Original spelling Chaenaina. *Chaena* is an unjustified emendation of *Gastrochaena* Spengler, 1783, and thus Chaenidae is an objective synonym of Gastrochaenidae.

CHAENOCARDIIDAE S. A. Miller, 1889 [after October]
Reference: *North American geology and palaeontology*: 458
Type genus: †*Chaenocardia* Meek & Worthen, 1869
Remarks: -inae, Newell (in Moore, ed., 1969: 339); -oidea / -ini, Waterhouse (2001: 123).

CHAENOMYINAE Waterhouse, 1966 [December]
Reference: *Journal of the Geological Society of Australia*, 13(2): 556
Type genus: †*Chaenomya* Meek [in Meek & Hayden], 1865
Remarks: -idae, Runnegar (1974: 925, 928); -ini, Waterhouse (2001: 147).

CHAMETRACHEIDAE H. Adams & A. Adams, 1857 [April]
Reference: *The Genera of Recent Mollusca*, 2: 464
Type genus: *Chametrachea* Mörch, 1853
Remarks: Original spelling Chametrachaeidae.

CHAMIDAE Lamarck, 1809
Reference: *Philosophie zoologique*: 318
Type genus: *Chama* Linnaeus, 1758
Remarks: Original spelling "Les camacées" (vernacular). First latinized, as Chamacea, by Children (1823: 27). Placed on the Official List

by Opinion 484 (1957: 75), but attributed in error to Blainville (1825: 541). -inae [as -ana], Bronn (1862: 475, 500); -oidea [as -acea], Gill (1871: 20).

CHAMOSTREIDAE Stoliczka, 1870 [1 September]
Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b
Type genus: *Chamostrea* Gray, 1840
Remarks: See Cleidothaeridae.

CHARTOCONCHINI Taktakishvili, 1987
Reference: *Sistematika i filogeniia plitsenykh cardiid Paratetisa*: 12, 179
Type genus: †*Chartoconcha* Andrusov, 1907
Remarks: Precedence of simultaneously published Pontalmyrini determined by First Reviser action by Nevesskaja et al. (2001: S191). -ina, Bieler, Carter & Coan, herein.

CHIAPASELLIDAE Alencaster, 1971
Reference: *Paleontologia Mexicana*, 34: 78
Type genus: †*Chiapasella* Müllerried, 1931

CHIONIDAE Frizzell, 1936 [June]
Reference: *Proceedings of the Geological Society of America*, (1935): 415
Type genus: *Chione* Megerle von Mühlfeld, 1811
Remarks: Name only, no description. Available under Art. 13.2.1 because it was subsequently used as valid by Frizzell (1936b: 65, with description). -inae, Keen (1951a: 9; 1951b: 6).

CHLAMYDINAE Teppner, 1922 [30 December]
Reference: *Fossilium Catalogus*, I, Pars 15: 101
Type genus: *Chlamys* Röding, 1798
Remarks: Original spelling Chlamiyinae. Attributed by Teppner to E. Philippi (1900: 85), who merely used the expression "Stamm *Chlamys*". Independently declared new by Korobkov (in Eberzin, 1960: 83, as Chlamysinae); by Masuda (1962: 149, 159, as Chlamiinae); and by F. Nordsieck (1969: 50, as Chlamysinae). -idae, Sobetskij (1982: 101); -ini, Beu & Darragh (2001: 2, 12, 38).

CHLAMYDOCONCHIDAE Dall, 1884 [18 July]
Reference: *Science*, 4(76): 51
Type genus: *Chlamydoconcha* Dall, 1884
Remarks: Original spelling Chlamydoconchae. -inae, Thiele (1934: 874); -oidea [as -acea], Keen (in Moore, ed., 1969: 537).

CHOKRAKIINI Popov, 2001

Reference: [in Nevesskaja, Paramonova & Popov] *Paleontological Journal*, 35, suppl. 3: 149, 178

Type genus: †*Chokrakia* Popov, 2001

Remarks: -ina, Bieler, Carter & Coan, herein.

CHONDRODONTIDAE Freneix, 1960 [February]

Reference: *Compte-Rendu du Congrès des Sociétés Savantes, Dijon 1959, Section des Sciences, Sous-section de Géologie*: 216

Type genus: †*Chondrodonta* Stanton, 1901

CHULUARIINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 55

Type genus: †*Chuluarina* Waterhouse, 2000

CINCLIDOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 24

Type genus: †*Cinclidoceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

CIRCINAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 552

Type genus: *Circe* Schumacher, 1817

Remarks: -idae [declared new], Frizzell (1936a: 415). Placed on the Official Index by Opinion 1189 (1981: 243) because of its homonymy with *Circinae* Sundevall, 1836, based on *Circus* [Aves]; see Gafrariinae.

CIRRAVIDAE Chernyshev, 1935

Reference: *Ezhegodnik Vserossiiskogo Paleontologicheskogo Obshchestva*, 10: 36

Type genus: †*Cirravus* Chernyshev, 1935

Remarks: Described as a Cirripedia [Crustacea], and treated as such in the Treatise, but listed by Urbajtis (1975: 133) as a bivalve.

CITOTHYRISIDAE Hajkr, Lukasová, Růžicka & Řehoř, 1974

Reference: *Freiberger Forschungshefte*, ser. C, 306: 68

Type genus: †*Citothyris* Růžicka & Řehoř, 1964

CLADOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 25

Type genus: †*Cladoceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description). Genus name *Cladoceramus* subsequently made available by Seitz, 1961, but this leaves Cladoceraminae unavailable.

CLARAIINAE Gavrilova, 1996

Reference: *Paleontologicheskii Zhurnal*, 1996(4): 12, 13

Type genus: †*Claraia* Bittner, 1901

Remarks: -ini, Waterhouse (2000: 159); -idae, Waterhouse (2008: 54).

CLAVAGELLIDAE d'Orbigny, 1844

Reference: *Paléontologie française. Terrains crétacés*, 3: 14 [1844], 299 [1845]

Type genus: †*Clavagella* Blainville, 1817

Remarks: Original spelling Clavagelidae. -inae [as -ina], Gray (1858b: 314); -oidea [as -acea], Haas (1929: 19). Under Art. 23.9 of the Code, Aspergillidae Burmeister, 1837, is here declared a *nomen oblitum* and Clavagellidae d'Orbigny, 1844, a *nomen protectum*, based on usage in at least the following publications: Appukuttan (1974: 19, 20), Azuma (1960: 95), Beu & Maxwell (1990: 152, 187, 402), Bruschi et al. (1985: 64), Eberzin (1960: 144), Franc (1960: 2127), Goto & Poppe (1996: 1018), Harper et al. (2000: 129, 132), Higo et al. (1999: 524), Higo & Goto (1993: 678), Kilburn (1974: 89), Kira (1962: 184), Kuroda et al. (1971: 728), Lambiotte (1978: 1), Macpherson & Gabriel (1962: 401), Matsumoto (1979: 116), Moore (1969: 857, 858), Morton (1982: 210, 211), Nevesskaja et al. (1971: 16), Newell (1965: 21), Pojeta & Sohl (1987: 57, 59), Savazzi (1982: 83; 2000: 313, 314), Scarlato & Starobogatov (1979a: 22), B. J. Smith (1971: 135; 1974: 187), L. A. Smith (1962: 167), Soliman (1971: 389), Starobogatov (1992: 21), Vaught (1989: 140), H. A. Vokes (1980: 214). To our knowledge, the name Aspergillidae has not been used as valid after 1899.

CLEIDOTHAERIDAE Hedley, 1918 [19 June] (1870)

Reference: *Journal and Proceedings of the Royal Society of New South Wales*, 51, supplement: M14

Type genus: *Cleidothaerus* Stutchbury, 1830

Remarks: When he established Cleidothaeridae, Hedley did not cite Chamostreidae, but *Chamostrea* is a synonym of *Cleidothaerus*. Cleidothaeridae is in prevailing usage; it is conserved under Art. 40.2 with the priority of Chamostreidae (1870).

CLEMENTIIDAE Frizzell, 1936 [June]

Reference: *Proceedings of the Geological Society of America*, (1935): 415

Type genus: *Clementia* Gray, 1842

Remarks: Name only, no description. Available under Art. 13.2.1 because it was subsequently used as valid by Frizzell (1936b: 64, with description). -inae, Keen (1951a: 9; 1951b: 5).

CLINOCARDIINAE Kafanov, 1975

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 5: 146, 147

Type genus: *Clinocardium* Keen, 1936

Remarks: -ini, same reference; -idae, Scarlato & Starobogatov (1979a: 23). Precedence over simultaneously established Serripedini determined by Art. 24.1 (subfamily vs tribe).

CLINOPISTHINAE Pojeta, 1988 [October]

Reference: *New Mexico Bureau of Mines & Mineral Resources, Memoir* 44: 216

Type genus: †*Clinopistha* Meek & Worthen, 1870

COALCOMANINAE Coogan, 1973 [April]

Reference: *Revista del Instituto Mexicano del Petroleo*, 5(2): 57

Type genus: †*Coalcomana* Harris & Hodson, 1922

COCHLEARITIDAE Benini & Loriga, 1977 [September]

Reference: *Bollettino della Società Paleontologica Italiana*, 16(1): 50

Type genus: †*Cochlearites* Reis, 1903

CODAKIIDAE Korobkov, 1954

Reference: *Spravochnik i metodicheskoe rukovodstvo po tretichnym molliuskam. Platinchatozhabernye*: 86

Type genus: *Codakia* Scopoli, 1777

Remarks: -inae, J. D. Taylor, herein (pers. com.).

COELATURINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 190

Type genus: *Coelatura* Conrad, 1853

Remarks: Original spelling Caelaturinae, based on *Caelatura* Simpson, 1900, an unjustified emendation of *Coelatura*; the original spelling of the type genus was discussed by Rosenberg et al. (1990: 29). -ini, Starobogatov (1970: 64).

COLONICERAMIDAE Pochialaynen, 1985

Reference: *Kolonitseramy v neokome na severe Patsifiki*: 10

Type genus: †*Coloniceramus* Pochialaynen, 1972

Remarks: Not available (no description) from Pochialaynen (1985b: 31).

COLPOMYIDAE Pojeta & Gilbert-Tomlinson, 1977 [December]

Reference: *Bureau of Mineral Resources, Geology and Geophysics [Canberra]. Bulletin* 174: 37

Type genus: †*Colpomya* Ulrich, 1894

CONCAVODONTINAE Sánchez, 1999 [25 January]

Reference: *Journal of Paleontology*, 73(1): 71

Type genus: †*Concavodonta* Babin & Melou, 1972

CONCENTRICHLAMYDINAE Romanov, 1985

Reference: *Jurskie Pectinoidy Iuga SSSR*: 154

Remarks: Not available: not based on an available genus name. Not made available by its subsequent use by Kasum-Zade (2003: 51, 84, as Concentricochlamydinae).

CONCHAE Lamarck, 1809

Reference: *Philosophie zoologique*: 318

Remarks: Original spelling “Les conqués” (vernacular). Latinized by Children (1823 [in 1822–1824]: 309) based on Lamarck’s (1818: 555) division “Les Conques” of “Conchifères lamellipèdes”, containing the genera *Cyclas*, *Cyrena*, *Galathea*, *Cyprina*, *Cytherea*, *Venus* and *Venericardia*. Spelling emended to (family) Conchacea by Blainville (1824) and to Conchidae by Broderip (1839). Not available as a family-group name: not based on a genus. See also Names above the family-group.

CONDYLOCARDIIDAE F. Bernard, 1896

Reference: *Bulletin du Muséum d’Histoire Naturelle* [Paris], 2: 195

Type genus: *Condylocardia* F. Bernard, 1896

Remarks: Original spelling “Condylocardiidés” (vernacular). First latinized by Cossmann (1902: 23). Placed on the Official List by Opinion 872 (1969: 216). -inae, Chavan (in Moore, ed., 1969: 558); -oidea, Nevesskaja et al. (1971: 17).

CONGERIOMORPHIDAE Saul, 1976 [13 February]
Reference: *Journal of Paleontology*, 50(1): 153

Type genus: †*Congeriomorpha* Stoyanow, 1948

CONOCARDIIDAE S. A. Miller, 1889 [after October]

Reference: *North American geology and palaeontology*: 458

Type genus: †*Conocardium* Bronn, 1834

Remarks: -oidea [as -acea], Cox (1960: 85). Established as a family of bivalves, but now included in the separate class Rostroconchia.

CONTRADENTINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 189

Type genus: *Contradens* Haas, 1913

Remarks: Precedence of simultaneously published Rectidentinae determined by First Reviser action by Brandt (1974: 287).

COOPERELLIDAE Dall, 1900 [December]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(5): 1061

Type genus: *Cooperella* P. P. Carpenter, 1864

Remarks: -inae, Abbott (1954: 421).

CORBICULIDAE Gray, 1847 [November]

Reference: *Proceedings of the Zoological Society of London*, 15: 184

Type genus: *Corbicula* Megerle von Mühlfeld, 1811

Remarks: Original spelling Corbiculadae. When he established Corbiculidae, Gray did not cite Cyrenidae and included both *Corbicula* and *Cyrena* Lamarck, 1818, as valid genera; *Cyrena* and *Corbicula* were not and are not currently regarded as synonyms, and Art. 40.2 does not apply. -inae [as -ina], Gray (1853: 220); -oidea [as -acea], Gill (1871: 19).

CORBINAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8y

Type genus: *Corbis* Cuvier, 1817

Remarks: -idae, Dall (1895a: 544). See Fimbriidae Nicol, 1950.

CORBULAMELLINAE H. A. Vokes, 1945 [10 October]

Reference: *Bulletin of the American Museum of Natural History*, 86: 6, 19

Type genus: †*Corbulamella* Meek & Hayden, 1857

CORBULIDAE Lamarck, 1818

Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 423, 466, 493

Type genus: *Corbula* Bruguière, 1797

Remarks: Original spelling “Les Corbulées” (vernacular). First latinized [as *Corbulea*] by Children (1823: 301). -inae [as -ana], Bronn (1862: 476, 502); -oidea, Healy (1995: 107, 108). See also Aloididae.

CORDICERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 12

Type genus: †*Cordiceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description). Genus name *Cordiceramus* subsequently made available by Seitz, 1961, but this leaves Cordiceraminae unavailable.

CORNEOCYCLADIDAE Hannibal, 1912 [12 June]

Reference: *Proceedings of the Malacological Society of London*, 10(2): 133

Type genus: *Corneocyclus* Férussac, 1818

COSTATOPLICATININAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 160

Type genus: †*Costatoplicatina* Waterhouse, 2008

COSTATORIIDAE Newell & Boyd, 1975 [3 January]

Reference: *Bulletin of the American Museum of Natural History*, 154: 152

Type genus: †*Costatoria* Waagen, 1906

COSTEININAE Vialov, 1983

Reference: *Doklady Akademii Nauk Ukrainskoi SSR*, ser. B, 11: 7

Type genus: †*Costeina* Vialov, 1965

COXICONCHIINAE Babin, 1977 [February]

Reference: *Geobios*, 10(1): 66

Type genus: †*Coxiconchia* Babin, 1966

Remarks: Original spelling Coxiconchinae. -idae, Scarlato & Starobogatov (1979a: 20).

CRASSADOMINI Waller, 1993 [November]
Reference: *American Malacological Bulletin*,
10(2): 207
Type genus: *Crassadoma* F. R. Bernard, 1986

CRASSATELLIDAE Férussac, 1822 [13 April]
Reference: *Tableaux systématiques des ani-
maux mollusques*: xlij
Type genus: *Crassatella* Lamarck, 1799
Remarks: Original spelling "les Crassatelles"
(vernacular). First latinized [as *Crassatel-
laceae*] by Menke (1828: 65). -inae, Chavan
(1952a: 120); -oidea [as -acea], Newell
(1965: 19).

CRASSATELLITIDAE Dall, 1895 [March]
Reference: *Transactions of the Wagner Free In-
stitute of Science of Philadelphia*, 3(3): 539
Type genus: †*Crassatellites* Krüger, 1823
Remarks: Not available (Art. 11.7.1.4): Type
genus not available under Art. 20.

CRASSINIDAE Gray, 1840b [16 October]
Reference: *Synopsis of the contents of the
British Museum*, ed. 42: 137, 150
Type genus: *Crassina* Lamarck, 1818
Remarks: See Astartidae.

CRASSOSTREIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*,
80: 21, 30
Type genus: *Crassostrea* Sacco, 1897
Remarks: -ini [declared new], Chiplonkar &
Badve (1979: 442); -inae [established inde-
pendently], Torigoe (1981: 324).

CREMNOCERAMINAE Heinz, 1932
Reference: *Mitteilungen aus dem Mineralo-
gisch-Geologischen Staatsinstitut in Ham-
burg*, 13: 13
Type genus: †*Cremnoceramus* Heinz, 1932
Remarks: Not available: no description, and
type genus not an available name under Art.
13.1.1 (no description). Genus name *Crem-
noceramus* subsequently made available by
Cox, in Moore, 1969: 315, but this leaves
Cremnoceraminae unavailable.

CRENATULINAE Gray, 1854 [1 May]
Reference: *Annals and Magazine of Natural
History*, ser. 2, 13(77): 418
Type genus: *Crenatula* Lamarck, 1803
Remarks: Original spelling *Crenatulina*.

CRENELLIDAE Gray, 1840b [16 October]
Reference: *Synopsis of the contents of the
British Museum*, ed. 42: 140, 151

Type genus: *Crenella* T. Brown, 1827
Remarks: -inae [as -ina], Gray (1854a: 417).
Crenellinae independently declared new by
F. Nordsieck (1969: 29).

CRENIPECTINIDAE Scarlato & Starobogatov,
1979
Reference: *Trudy Zoologicheskogo Instituta*,
80: 20, 29
Type genus: †*Crenipecten* Hall, 1883
Remarks: -inae [declared new], Astafieva
(1991: 19).

CRENOMYTILINI Kafanov, 1984
Reference: *Tezisy dokladov vsesoiuznogo
soveshchaniia po teme: "Morfologia, sistema-
tika, filogeniia i ekogenez dvustvorchatykh
molliuskov"*: 45
Type genus: *Crenomytilus* Soot-Ryen, 1955

CRICOCERAMINAE Heinz, 1932
Reference: *Mitteilungen aus dem Mineralo-
gisch-Geologischen Staatsinstitut in Ham-
burg*, 13: 19
Type genus: †*Cricoceramus* Heinz, 1932
Remarks: Not available: no description, and
type genus not an available name under Art.
13.1.1 (no description).

CRYPTODONTIDAE Dall, 1895 [March]
Reference: *Transactions of the Wagner Free In-
stitute of Science of Philadelphia*, 3(3): 546
Type genus: *Cryptodon* Turton, 1822
Remarks: See Thyasiridae.

CRYPTOMYINAE Habe, 1977
Reference: *Systematics of Mollusca in Japan
(Bivalvia and Scaphopoda)*: 279
Type genus: *Cryptomya* Conrad, 1849

CRYPTOSTREINI Harry, 1985 [1 October]
Reference: *The Veliger*, 28(2): 143
Type genus: *Cryptostrea* Harry, 1985

CTENODONTIDAE Wöhrmann, 1893
Reference: *Jahrbuch der Kaiserlich-Königlichen
Geologischen Reichsanstalt*, 43(1): 28
Type genus: †*Ctenodonta* Salter, 1852
Remarks: -inae [declared new], Babin (1966:
41); -oidea, McAlester (in Moore, ed., 1969:
227).

CTENOSTREONINAE Kasum-Zade, 2003
Reference: [Advance in research of Mesozoic
bivalve mollusks in Azerbaijan Order Pectino-
ida: revision and systematics]: 60, 87
Type genus: †*Ctenostreon* Eichwald, 1862

CUCULLAEINAE Stewart, 1930 [9 August]

Reference: *The Academy of Natural Sciences of Philadelphia, Special Publication* 3: 74

Type genus: *Cucullaea* Lamarck, 1801

Remarks: -idae, Stephenson (1953: 62).

CUCULARIINAE Habe, 1977

Reference: *Systematics of Mollusca in Japan (Bivalvia and Scaphopoda)*: 42

Type genus: †*Cucullaria* Conrad, 1869

Remarks: Original spelling Cucullarinae.

CUCULLELLINAE P. Fischer, 1886 [30 April]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (10): 981

Type genus: †*Cucullella* M'Coy, 1851

Remarks: -idae, G. Termier & H. Termier (1950: 80, 82).

CUCUMERUNIONINAE Iredale, 1934 [9 May]

Reference: *The Australian Zoologist*, 8(1): 58, 77

Type genus: *Cucumerunio* Iredale, 1934

Remarks: Priority of simultaneously established Propehyridellidae determined by Art. 24.1 (family vs subfamily). -ini, Graf & Cummings (2006: 394, in synonymy of Hyridellini).

CUTELLIDAE Davies, 1935

Reference: *Tertiary faunas*, 1: 145

Type genus: *Cutellus* Schumacher, 1817

Remarks: Not available from "Cutellidés" (vernacular) of Douvillé (1912: 1681). -inae, Keen (1963: 92).

CUMBERLANDIINAE Heard & Guckert, 1970 [December]

Reference: *Malacologia*, 10(2): 338

Type genus: *Cumberlandia* Ortmann, 1912

Remarks: Original spelling Cumberlandinae.

CUMINGIINAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b, 106

Type genus: *Cumingia* G. B. Sowerby I, 1833

CUNEAMYINAE N. J. Morris, Dickins & Astafieva-Urbaitis, 1991

Reference: *Bulletin of the British Museum (Natural History)*, Geology Series, 47(1): 93

Type genus: †*Cuneamya* Hall & Whitfield, 1875

CUNEARCIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 23

Type genus: *Cunearca* Dall, 1898

CUNEOPSINAE Mongin, 1963

Reference: *Mémoires de la Société Géologique de France*, new ser., 42(1): 19

Type genus: *Cuneopsis* Simpson, 1900

Remarks: Not available: introduced conditionally.

CUNINAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 560

Type genus: *Cuna* Hedley, 1902

Remarks: Not available (no description) from Iredale & McMichael (1962: 16, as Cunidae). Abbott (1974: 479) attributed the name Cuni-nae to Laseron (1953: 33), who merely used a heading "The *Cuna* group of genera".

CURTONOTIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 538

Type genus: †*Curtonotus* Salter, 1862

Remarks: Invalid: Type genus a junior homonym of *Curtonotus* Stephens, 1827 [Crustacea].

CURVOSTREINI Malchus, 1990

Reference: *Berliner Geowissenschaftliche Abhandlungen*, ser. A, 125: 151

Type genus: †*Curvostrea* Vialov, 1936

CUSPIDARIIDAE Dall, 1886 [September]

Reference: *Bulletin of the Museum of Comparative Zoology*, 12(6): 196, 292

Type genus: *Cuspidaria* Nardo, 1840

Remarks: -oidea, Starobogatov (1970: 89).

CYAMIIDAE G. O. Sars, 1878

Reference: *Mollusca regionis arcticae Norvegiae*: 65

Type genus: *Cyamium* Philippi, 1845

Remarks: -oidea [as -acea], Thiele (1934: 857); -inae, Powell (1979: 399). The name Cyamidae is sometimes (e.g., by H. A. Vokes, 1980: 115) attributed to "Philippi, 1845", but Philippi established the genus name *Cyamium*, which he (Philippi, 1853: 345–346) placed in the family Lucinidae.

CYAMIOMACTRIDAE Iredale & McMichael, 1962 [30 May]

Reference: *The Australian Museum, Sydney, Memoir* 11: 20

Type genus: *Cyamiomactra* F. Bernard, 1897

Remarks: Not available: no description.

CYAMIONEMATIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 23, 34

Type genus: *Cyamionema* Melvill & Standen, 1914

CYCLADINAE Rafinesque, 1820 [September]

Reference: *Annales Générales des Sciences Physiques* [Bruxelles], 5: 318

Type genus: *Cyclas* Lamarck, 1798

Remarks: Original spelling (subfamily) Cycladia. -idae [as -ina], Berthold (1827: 209); -oidea, Scarlato & Starobogatov (1979a: 22). Invalid: placed on the Official Index by Direction 117 (1985: 43). See Sphaeriinae.

CYCLININAE Frizzell, 1936 [June]

Reference: *Proceedings of the Geological Society of America*, (1935): 415

Type genus: *Cyclina* Deshayes, 1850

Remarks: Name only, no description. Available under Art. 13.2.1 because it was subsequently used as valid by Frizzell (1936b: 64, with description).

CYCLOCONCHIDAE Ulrich, 1894 [16 June]

Reference: *The Geological and Natural History Survey of Minnesota*, vol. 3(2) [*Paleontology*]: 487, 617

Type genus: †*Cycloconcha* S. A. Miller, 1874

Remarks: -oidea [as -acea], Newell (in Moore, ed., 1969: 399).

CYCLOCONCHOIDIDAE Zhang, 1980

Reference: *Bulletin of the Chinese Academy of Geological Sciences*, ser. 8, 1(1): 12

Type genus: †*Cycloconchoides* Zhang, 1980

Remarks: Described as a bivalve but "it is unlikely that *Cycloconchoides* was either a pelecypod or a brachiopod" (Pojeta, 2001: 161).

CYMATOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 20

Type genus: †*Cymatoceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

CYPRICARDIIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science, Philadelphia*, 3(3): 538

Type genus: *Cypricardia* Lamarck, 1819

Remarks: Original spelling (superfamily) Cypricardiacea. -idae, Koken (1896: 175, 204). See Trapezidae.

CYPRICARDINIIDAE Ulrich, 1894 [16 June]

Reference: *The Geological and Natural History Survey of Minnesota*, vol. 3(2) [*Paleontology*]: 486

Type genus: †*Cypricardinia* Hall, 1859

CYPRINIADEIDAE Rovereto, 1900

Reference: *Atti della Reale Università di Genova*, 15: 96

Type genus: *Cypriniadea* Rovereto, 1900

Remarks: Original spelling Cypriniadeadae. Rovereto established *Cypriniadea* as a replacement name for *Cyprina*, by him believed to be a junior homonym of "Cyprina Linnaeus, 1758" [in reality *Cyprinus* (Pisces)]; and also for *Arctica* Schumacher, 1817, which he believed to be a junior homonym of "Arctica Möhr, 1752" [Aves; not an available name]; however, *Arctica* Schumacher, 1817, is not invalid, and *Cypriniadea* and Cypriniadeidae are unnecessary replacement names.

CYPRINIDAE d'Orbigny, 1844

Reference: *Paléontologie française. Terrains crétacés*, 3(1): 14

Type genus: *Cyprina* Lamarck, 1818

Remarks: Junior homonym of Cyprinidae Rafinesque, 1815, based on *Cyprinus* Linnaeus, 1758 [Pisces]. Under Art. 55.3, Cyprinidae d'Orbigny, 1844, is a potentially valid name, but Arctidae, which is in prevailing usage, is conserved under Art. 40.2 (see Boss 1969: 61); see Arctidae. -inae [as -ana], Bronn (1862: 476, 500); -oidea [as -acea], Steinmann (1903: 234, 239).

CYPROGENIINAE Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 70, 287

Type genus: *Cyprogenia* Agassiz, 1852

CYRENELLIDAE Gray, 1853 [1 January]

Reference: *Annals and Magazine of Natural History*, ser. 2, 11(61): 39

Type genus: *Cyrenella* Deshayes, 1836

Remarks: Original spelling Cyrenelladae. See also Cyrenoididae.

CYRENIDAE Gray, 1840b [16 October]

Reference: *Synopsis of the contents of the British Museum*, ed. 42: 133, 149

Type genus: *Cyrena* Lamarck, 1818

Remarks: -inae [as -ana], Bronn (1862: 476, 501); -oidea [as -acea], Tryon (1884: 184). See also Geloinidae.

CYRENOIDIDAE H. Adams & A. Adams, 1857
[April] (1853)

Reference: *The Genera of Recent Mollusca*, 2: 452

Type genus: *Cyrenoida* Joannis, 1835

Remarks: *Cyrenella* Deshayes, 1836 was established in synonymy of *Cyrenoida*, and H. & A. Adams have probably introduced Cyrenoididae to replace Cyrenellidae (which, however, they did not cite). Cyrenoididae is in prevailing usage and is conserved under Art. 40.2, with the priority of Cyrenellidae (1853).-inae [as -ana], Bronn (1862: 476, 501); -oidea [as -acea], Olsson (1961: 227).

CYRTODONTIDAE Ulrich, 1894 [16 June]

Reference: *The Geological and Natural History Survey of Minnesota*, vol. 3(2) [*Paleontology*]: 486, 533

Type genus: †*Cyrtodonta* Billings, 1858

Remarks: -oidea [as -acea], Newell (1965: 17).

CYRTOROSTRIDAE Newell & Boyd, 1995 [13 December]

Reference: *Bulletin of the American Museum of Natural History*, 227: 62

Type genus: †*Cyrtorostra* Branson, 1930

Remarks: -inae, Waterhouse (2001: 130).

CYTHEREINAE Gray, 1838

Reference: *The Analyst*, 8: 302

Type genus: *Cytherea* Lamarck, 1805

Remarks: Original spelling Cythereina. *Cytherea* was used by Lamarck, 1805, as a substitute name for *Meretrix* Lamarck, 1799, and is not the same as *Cytherea* Röding, 1798 [= *Periglypta* Jukes-Browne, 1914]. -idae [as Cytheridae], d'Orbigny (in Webb & Berthelot, 1840: 106). Invalid: type genus a junior homonym of *Cytherea* Fabricius, 1794 [Diptera]. See Meretricinae.

CYTHERODONTIDAE S. A. Miller, 1877

Reference: *The American Palaeozoic fossils*: 180

Type genus: †*Cytherodon* Hall & Whitfield, 1873

DACRYDIINAE Ockelmann, 1983 [June]

Reference: *Ophelia*, 22(1): 112

Type genus: *Dacrydium* Torell, 1859

DACTYLOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 23

Type genus: †*Dactyloceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

DALLICORDIIDAE Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 12

Type genus: *Dallicordia* Scarlato & Starobogatov, 1983

DANLENGICONCHINAE Sha, 1993

Reference: [Sha Jin-geng] *Acta Palaeontologica Sinica*, 32(3): 290 [Chinese], 300 [English]

Type genus: †*Danlengiconcha* Liu, 1978

Remarks: Original spelling Danlengiconchinae.

DAONELLIDAE Neumayr, 1891

Reference: *Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 58: 724

Type genus: †*Daonella* Mojsisovics, 1874

Remarks: Original spelling "Daonelliden" (vernacular). First latinized by Grobben (1892a: 142; 1892b: 373).

DATTIDAE Healey, 1908

Reference: *Memoirs of the Geological Survey of India. Paleontologia Indica*, new ser., 2(4): 63

Type genus: †*Datta* Healey, 1908

DAVILINAE Dall, 1895 [March]

Reference: *Proceedings of the Malacological Society of London*, 1(5): 209, 213

Type genus: *Davila* Gray, 1853

DECATOPECTININI Waller, 1986 [30 April]

Reference: *The Nautilus*, 100(2): 40

Type genus: *Decatopecten* Sowerby II, 1839

Remarks: -inae [declared new], Kasum-Zade (2003: 48, 83).

DELTOPECTINIDAE Dickins, 1957 [31 July]

Reference: *Bureau of Mineral Resources, Geology and Geophysics [Canberra], Bulletin*, 41: 39

Type genus: †*Deltopecten* Etheridge, 1892

Remarks: -inae, Waterhouse (2001: 128).

DENTASPATHARIINAE Modell, 1964 [20 July]

Reference: *Archiv für Molluskenkunde*, 93(3–4): 83

Type genus: †*Dentaspatharia* Modell, 1964

Remarks: Modell declared *Dentaspathariinae* as a “nom. nov.” and cited *Pseudaviculinae* Modell, 1942, as a synonym. However, the type species of *Dentaspatharia* is *Unio galloprovincialis* Matheron, 1842, from the Cretaceous of France, whereas the type species of *Pseudavicula* Simpson, 1900, non Huxley, 1890, is the Recent *Unio johnstoni* E.A. Smith, 1893, from Central Africa. Thus, *Dentaspathariinae* is not a nomenclatural replacement name for *Pseudaviculinae*, but a taxonomically separate family-group name. See also *Prisodontopsinae*.

DERMATOMYIDAE Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 11

Type genus: *Dermatomya* Dall, 1889

Remarks: -oidea, same reference.

DESERTELLIDAE Dechaseaux, 1947 [January]

Reference: *Compte-Rendu Sommaire des Séances de la Société Géologique de France*, 1946(15): 307

Type genus: †*Desertella* Haug, 1905

DEXIOBIINAE Newell & LaRocque, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 246

Type genus: †*Dexiobia* Winchell, 1863

Remarks: -idae, Nevesskaja (2003: 616).

DEXTRODONTA. See higher category list.

DIANCHORIDAE Sobetski, 1977

Reference: *Trudy Paleontologicheskogo Instituta*, 159: 81

Type genus: †*Dianchora* J. Sowerby, 1815

DICERATIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 542

Type genus: †*Diceras* Lamarck, 1805

Remarks: -inae, Anthony (1905: 286, 373, 383); -oidea [as -acea], H. A. Vokes (1967: 232).

DICEROCARDIIDAE Kutassy, 1934 [31 December]

Reference: *Fossilium Catalogus*, I, Pars 68: 62

Type genus: †*Dicerocardium* Stoppani, 1865

Remarks: Name only, no description. Available under Art. 13.2.1 through its use as a valid name by, e.g., Cox (in Moore, ed., 1969: 658).

DICTYOPTYCHIDAE Skelton, 1993

Reference: [in Skelton & Benton] *The fossil record*, 2: 258

Type genus: †*Dictyoptychus* Douvillé, 1905

Remarks: Established as a substitute name for “*Trechmanellinae* MacGillavry, 1937” [in fact Cox, 1934].

DIDACNINAE Eberzin, 1962

Reference: *Trudy Paleontologicheskogo Instituta*, 91: 26

Type genus: *Didacna* Eichwald, 1838

Remarks: Established independently by F. Nordsieck (1969: 106). -ini, Kafanov & Popov (1977: 60).

DIGRESSODACNINI Taktakishvili, 1987

Reference: *Sistematika i filogeniia plitsenykh cardiid Paratetisa*: 12, 118

Type genus: †*Digressodacna* Davitaschvili & Kitovani, 1964

Remarks: Priority of simultaneously published Pontalmyrini determined by First Reviser action by Nevesskaja et al. (2001: S191). -ina, Bieler, Carter & Coan, herein.

DIMYIDAE P. Fischer, 1886 [30 April]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (10): 936

Type genus: †*Dimya* Rouault, 1850

Remarks: -inae, Frech (1891: 409 [149]); -oidea [as -acea], Habe (1951: 69).

DINOCARDIINI Kafanov, 1977

Reference: [in Kafanov & Popov] *Paleontologicheskii Zhurnal*, 1977(3): 62

Type genus: *Dinocardium* Dall, 1900

DIPLASMINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 177

Type genus: *Diplasma* Rafinesque, 1831

Remarks: See also *Hemisolasminae*.

DIPLODONTIDAE P. P. Carpenter, 1861

Reference: *Annual Report of the Board of Regents of the Smithsonian Institution for 1860*: 261

Type genus: *Diplodonta* Bronn, 1831

DIPLODONTIDAE Ihering, 1901 [3 September]

Reference: *The Nautilus*, 15(5): 52

Type genus: *Diplodon* Spix, 1827

Remarks: -inae, Morretes (1949: 17); -ini, Parodiz & Bonetto (1963: 199, 204). Homonym of *Diplodontidae* P. P. Carpenter, 1861,

based on *Diplodonta*; under Art. 55.3, the case should be referred to the ICZN. See Rhipidodontini.

DIVARICELLIDAE Korobkov, 1954

Reference: *Spravochnik i metodicheskoe rukovodstvo po tretichnym molliuskam. Platinchatozhabernye*: 87

Type genus: *Divaricella* Martens, 1880

Remarks: -inae, Chavan (in Moore, ed., 1969: 506).

DOLPONELLIDAE Waterhouse, 2001 [1 July]

Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 135

Type genus: †*Dolponella* Waterhouse, 1978

DONACIDAE J. Fleming, 1828 [March]

Reference: *A history of British animals*: 409

Type genus: *Donax* Linnaeus, 1758

Remarks: -inae, H. Adams & A. Adams (1856: 403); -oidea, Nevesskaja et al. (1971: 16).

DONACILLIDAE Macpherson & Gabriel, 1962

Reference: *Marine molluscs of Victoria*: 359

Type genus: *Donacilla* Blainville, 1819

DOSINIINAE Deshayes, 1853

Reference: [in Gray, ed.] *Catalogue of the Conchifera or bivalve shells in the collection of the British Museum. I, Veneridae*: 3, 5

Type genus: *Dosinia* Scopoli, 1777

Remarks: Original spelling Dosiniana. -idae [declared new], Frizzell (1936a: 415).

DREISSENIDAE Gray, 1840a [between March and June]

Reference: [new edition of Turton] *A manual of the land and fresh-water shells of the British Islands*: 277, 299

Type genus: *Dreissena* van Beneden, 1835

Remarks: Original spelling Driessenadae (p. 277) and Dreissenadae (p. 299). -inae [as Dreissensiana], Bronn (1862: 474, 499); -oidea [as -acea], Gill (1871: 19). Placed on the Official List by Direction 41 (1956: 433).

DREISSENOMYINAE Babak, 1983

Reference: *Trudy Paleontologicheskogo Instituta*, 204: 18, 59, 60

Type genus: †*Dreissenomya* Fuchs, 1870

Remarks: First established as “Dreissenomyidés” (vernacular) by Bolgiu (1945: 411). Not available from Taktakishvili (1973: 12, 13) who, in a discussion of Bolgiu’s work, latinized the name but did not use it as the valid name of a taxon.

DROMINI Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental’nykh vodoemov zemnogo shara*: 70, 287

Type genus: *Dromus* Simpson, 1900

DUALINIDAE Conrath, 1887 [14 July]

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 96(1): 49

Type genus: †*Dualina* Barrande, 1881

Remarks: -inae, same reference. Precedence over simultaneously established Praeluciniidae determined by First Reviser action, J. Kříž (pers. com.), herein.

DURANIIDAE Yanin, 1990 [before 22 October]

Reference: [in Menner ed.] *Sistematika i filogeniia bespozvonochnykh. Kriterii vydeleniia vyschikh taksonov*: 66

Type genus: †*Durania* Douvillé, 1908

EBURNEOPECTININI Waller, 2006

Reference: [in Shumway & Parsons, eds] *Scallops: Biology, ecology and aquaculture*: 8, 14

Type genus: †*Eburneopecten* Conrad, 1865

Remarks: Original spelling Eburneopectenini. Not available (no description) from Vaught (1989: 119, as Eburneopectenini).

ECHINIFERIPECTININAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 78

Type genus: †*Echiniferipecten* Waterhouse, 2008

ECHINORBINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 130

Type genus: †*Echinorbis* Waterhouse, 1987

Remarks: -ini, Waterhouse, same reference.

EDENTULOIDEA Cossmann, 1909

Reference: [in Cossmann & Peyrot] *Actes de la Société Linnéenne de Bordeaux*, 63(3): 148

Remarks: Original spelling (“Cénacle” = superfamily) Edentulacea, containing the family Gastrochaenidae only. Not available (not based on a genus).

EDMONDIIDAE King, 1850

Reference: *A monograph of the Permian fossils of England*: 162

Type genus: †*Edmondia* de Koninck, 1841

Remarks: -oidea [as -acea], Newell (1965: 17); -ini [as -ides], Waterhouse (1969: 21).

ELIGMIDAE Gill, 1871 [February]

Reference: *Smithsonian Miscellaneous Collections*, 227: 22

Type genus: †*Eligmus* Eudes-Deslongchamps, 1856

Remarks: Heligminae is an incorrect subsequent spelling based on *Heligmus* P. Fischer, 1885, an unjustified emendation of *Eligmus*. First used as “Héligminés” (vernacular) by P. Fischer (1885: 928), and latinized by Cossman (1908: 32).

ELLIPTIONIDAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 178, 180

Type genus: *Elliptio* Rafinesque, 1819

Remarks: -inae, same reference.

ELYMELLIDAE Ulrich, 1894 [16 June]

Reference: *The Geological and Natural History Survey of Minnesota*, vol. 3(2) [*Paleontology*]: 486

Type genus: †*Elymella* Hall, 1885

ENFERMÉS Cuvier, 1817

Reference: *Le règne animal ...*, 2: 487

Remarks: Established as a family including the genera *Mya*, *Lutraria*, *Anatina*, *Glycymeris*, *Solen*, *Teredo*, etc. Vernacular name only; later latinized as Tubicolidae. Not available: not based on a genus.

ENOCEPHALIDAE de Stefani, 1880

Reference: *Atti della Società Toscana di Scienze Naturali Residente in Pisa, Memorie*, 5: 62, 63

Type genus: †*Enocephalus* Goldfuss, 1837

ENSIPHONACEA Dall, 1889 [December]

Reference: *The American Journal of Science*, ser. 3, 38: 457, 460

Remarks: Established as a suborder (see higher category list). Used by Dall (1895a: 534) as a superfamily containing the family Clavagellidae only. Not available as a family-group name (not based on a genus).

ENTOLIINAE Teppner, 1922 [30 December]

Reference: *Fossilium Catalogus*, I, Pars 15: 89

Type genus: †*Entolium* Meek, 1865

Remarks: Attributed by Teppner to E. Philippi (1900: 77), who however merely used the expression “Stamm *Entolium*”. Established independently by Korobkov (in Eberzin, 1960: 83). -idae, Newell (1965: 18).

ENTOLIOIDESINAE Kasum-Zade, 2003

Reference: [*Advance in research of Mesozoic bivalve mollusks in Azerbaijan Order Pectinoida: revision and systematics*]: 43, 82

Type genus: †*Entolioides* Allasinaz, 1972

Remarks: -idae [as Entolioididae, declared new], Waller (2006b: 313, 320).

EOASTARTIDAE Newell & Boyd, 1975 [3 January]

Reference: *Bulletin of the American Museum of Natural History*, 154: 130

Type genus: †*Eoastarte* Ciriacks, 1963

Remarks: -inae, M. R. Cooper (1991: 4). Precedence of simultaneously published Schizodidae determined by First Reviser action by Boyd & Newell (1997: 6).

EOCAMPTONECTINI Waterhouse, 2001 [1 July]

Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 131

Type genus: †*Eocamptonectes* Newell, 1969

EODONIDAE Carter, D. C. Campbell & M. R. Campbell, 2000 [12 December]

Reference: [in Harper, Taylor & Crame, eds.] *The evolutionary biology of the Bivalvia*: 62, 64

Type genus: †*Eodon* Hall, 1877

EOMIODONTINAE Hayami, 1965 [20 December]

Reference: *Memoirs of the Faculty of Science, Kyushu University*, ser. D, *Geology*, 17(2): 129

Type genus: †*Eomiodon* Cox, 1935

EOPTERIIDAE S. A. Miller, 1889 [after October]

Reference: *North American geology and palaeontology*: 458

Type genus: †*Eopteria* Billings, 1865

Remarks: -oidea [as -acea], Pojeta & Runnegar (1976: 47). Established as a family of bivalves, but now included in the separate class Rostroconchia.

EOSCHIZODIDAE Newell & Boyd, 1975 [3 January]

Reference: *Bulletin of the American Museum of Natural History*, 154: 90

Type genus: †*Eoschizodus* Cox, 1951

Remarks: -inae, M. R. Cooper (1991: 4).

EPHIPPODONTIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 23, 34

Type genus: *Ehippodonta* Tate, 1889

Remarks: Original spelling Ehippiodontidae, based on *Ehippiodontia*, an incorrect subsequent spelling of *Ehippodonta*.

EPICERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 25

Type genus: †*Epiceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

EPIDICERATIDAE Rengarten, 1950

Reference: *Trudy Instituta Geologicheskikh Nauk*, 130 [Ser. *Geologicheskaja*, 51]: 2, 5

Type genus: †*Epidiceras* Dechaseaux, 1952

Remarks: Name only, no description. Available through its use as a valid name by, e.g., Bolkova & Pchelintsev (in Eberzin, ed., 1960: 154 [with description]). -inae, Coogan (in Moore, ed., 1969: 779); -oidea, Yanin (1990: 64).

ERIPHYLINAE Chavan, 1952

Reference: *Cahiers Géologiques de Thoiry*, 15: 126

Type genus: †*Eriphyla* Gabb, 1864

ERITROPIDAE Cope, 2000 [12 December]

Reference: [in Harper, Taylor & Crame, eds.] *The evolutionary biology of the Bivalvia*: 88

Type genus: †*Eritropis* Pojeta & Gilbert-Tomlinson, 1977

ERODONIDAE Winckworth, 1932 [June]

Reference: *Journal of Conchology*, 19(7): 246

Type genus: *Erodona* Bosc, 1802

Remarks: Name only, no description. Available through its use as a valid name by, e.g., Keen (in Moore, ed., 1969: 698, with diagnosis, and name attributed to Winckworth).

ERVILIINAE Dall, 1895 [March]

Reference: *Proceedings of the Malacological Society of London*, 1(5): 210, 213

Type genus: *Ervilia* Turton, 1822

ERYCINIDAE Deshayes, 1850

Reference: *Traité élémentaire de conchyliologie*, 1(2): 718

Type genus: †*Erycina* Lamarck, 1805

Remarks: -oidea [as -acea], Cossmann & Peyrot (1912: 544); -inae, Thiele (1934: 869). Junior homonym of Erycinidae Swainson, 1827, based on *Erycina* Fabricius, 1807 [Lepidoptera].

ETHERIIDAE Deshayes, 1832 [29 September]

Reference: *Encyclopédie méthodique. Histoire naturelle des vers*, 2: unnumbered table with pp. 471–553

Type genus: *Etheria* Lamarck, 1807

Remarks: Original spelling “Ethéries” (vernacular). First latinised (as Etheridae) by Swainson (1840: 390), but generally attributed to Deshayes, e.g. by Starobogatov (1970) and Graf (2000). Aetheriidae [Herrmannsen, 1846: 24] is an incorrect spelling based on the unjustified emendation *Aetheria* Oken, 1818. Priority of simultaneously published Mulleriidae determined by First Reviser action by Gill (1871: 20). -oidea [as Aetheriacea], Tryon (1884: 244); -inae, Modell (1942: 177).

ETHERIPECTININAE Waterhouse, 1982

Reference: *New Zealand Geological Survey Paleontological Bulletin*, 49: 15

Type genus: †*Etheripecten* Waterhouse, 1963

Remarks: -idae, Newell & Boyd (1995: 33); -ini, Waterhouse (2001: 116, 120); -oidea, Waterhouse (2008: 134).

EUCHARIDAE Récluz, 1869

Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): unpaginated table between pp. 34 and 35

Type genus: *Eucharis* Récluz, 1850

Remarks: Invalid: Type genus a junior homonym of *Eucharis* Latreille, 1804 [Hymenoptera].

EUCHASMIDAE Starobogatov, 1977

Reference: *Biulleten' Moskovskogo Obshchestva Ispitatelei Priroda, Otdel Geologicheskii*, 52(4): 136

Type genus: †*Euchasma* Billings, 1865

Remarks: -oidea, same reference. Established as a family of bivalves, but now classified in the separate class Rostroconchia.

EUCHONDRIIDAE Newell, 1938 [28 July]

Reference: *State Geological Survey of Kansas Publications*, 10(1): 102

Type genus: †*Euchondria* Meek, 1874

Remarks: -inae, Eberzin (1960: 82); -oidea, Nevesskaja et al. (1971: 15).

EUCIROIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 535

Type genus: *Euciroa* Dall, 1881

Remarks: -oidea, Scarlato & Starobogatov (1983: 9).

EUCRASSATELLIDAE Iredale & McMichael, 1962
 Reference: *The Australian Museum, Sydney. Memoir* 11: 16
 Type genus: *Eucrassatella* Iredale, 1924
 Remarks: Not available: no description.

EUGENOCERAMINAE Heinz, 1932
 Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 24
 Type genus: †*Eugenoceramus* Heinz, 1932
 Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

EUGLESINAE Pirogov & Starobogatov, 1974
 Reference: *Zoologicheskii Zhurnal*, 53(3): 327
 Type genus: *Euglesa* Jenyns, 1832
 Remarks: -idae, Starobogatov & Korniushev (1989: 13, 19).

EULOXIDAE J. A. Gardner, 1943
 Reference: *United States Geological Survey Professional Paper*, 199A: 65
 Type genus: †*Euloxa* Conrad, 1863
 Remarks: Name only, no description. Available through its use as a valid name by, e.g., Keen (in Moore, ed., 1969: 650, with diagnosis, and name attributed to Gardner).

EUNYMPHACEA Cossmann, 1910 [8 October]
 Reference: [in Cossmann & Peyrot] *Actes de la Société Linnéenne de Bordeaux*, 64(5): 292
 Remarks: Established as a “cénacle” (= superfamily), containing the families Psammobiidae and Donacidae. Not available as a family-group name (not based on a genus).

EUPECTININAE Teppner, 1922 [30 December]
 Reference: *Fossilium Catalogus*, I, Pars 15: 142
 Remarks: Name attributed by Teppner to E. Philippi (1900: 93), who however merely used the expression “Der Stamm der *Eupecten*”. Not available (not based on a genus).

EUPERINAE Heard, 1965 [October]
 Reference: *The American Midland Naturalist*, 74(2): 309
 Type genus: *Eupera* Bourguignat, 1854
 Remarks: -idae, Scarlato & Starobogatov (1979a: 22).

EURYDESMATIDAE Reed, 1932
 Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica*, new ser., 20(1): 50

Type genus: †*Eurydesma* J. Morris, 1845
 Remarks: Original spelling Eurydesmidae. No description, but available under Art. 13.2.1 through its use as a valid name by Reed (1936: 16). -oidea, Waterhouse (2001: 135).

EUSIPHONIA Dall, 1895 [March]
 Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 530
 Remarks: Established as a division of the superfamily Anatioidea including the families Ceromyidae, Pholadomyidae, Anatinidae, Periplomatidae, Thraciidae and Myochamidae. Not available as a family-group name (not based on a genus).

EUUNIONIDAE Amalitsky, 1892 [November]
 Reference: *Palaeontographica*, 39(4–6): 201
 Remarks: Not available: not based on a genus.

EUXINIBARNEINI Zhgenti, 1991
 Reference: *Evoliutsiia i stratigraficheskoe znachenie molliuskovoi fauny konskogo Iarusa Gruzii*: 57
 Type genus: †*Euxinibarnea* Zhgenti, 1966
 Remarks: Original spelling Euxinibarnini.

EVYANIDAE Carter, D. C. Campbell & M. R. Campbell, 2000 [12 December]
 Reference: [in Harper, Taylor & Crame, eds.] *The evolutionary biology of the Bivalvia*: 59, 63
 Type genus: †*Evyana* Liljedahl, 1990

EXOXYRINAE Vialov, 1936 [4 October]
 Reference: *Doklady Akademii Nauk SSSR*, ser. 2, 4(1): 20
 Type genus: †*Exogyra* Say, 1820
 Remarks: -ini, Stenzel (in Moore, ed., 1971: 1115); -idae, Scarlato & Starobogatov (1979a: 21); -oidea, Sobetski (1982: 134).

FALCATODONTIDAE Cope, 1996 [December]
 Reference: *Palaeontology*, 39(4): 1012, 1013
 Type genus: †*Falcatodonta* Cope, 1996
 Remarks: -oidea, same reference.

FERGANOCONCHIDAE Martinson, 1961
 Reference: *Trudy Baikalskoi Limnologicheskoi Stantsii*, 19: 166
 Type genus: †*Ferganoconcha* Ljutkevitch & Nalivkin, 1960
 Remarks: Not available from Martinson (1956: 59): Martinson attributed *Ferganoconcha* to Chernyshev, 1937, but no type species was designated until Ljutkevitch & Nalivkin, 1960,

which means that the name was not available when it was used as the type genus of *Ferganoconchidae* by Martinson (1956).

FERRAZIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 22, 32

Type genus: †*Ferrazia* Reed, 1932

FIMBRIIDAE Nicol, 1950 (1870)

Reference: *Journal of the Washington Academy of Sciences*, 40(3): 82

Type genus: *Fimbria* Megerle von Mühlfeld, 1811

Remarks: Established as a replacement name for *Corbidae* because Nicol treated *Corbis* Cuvier, 1817, as a synonym of *Fimbria*. *Fimbriidae* is in prevailing usage; it is conserved under Art. 40.2, with the priority of *Corbidae* (1870). Homonym of *Fimbriidae* O'Donoghue, 1926, based on *Fimbria* O'Donoghue, 1926 [ex Bohadsch, 1761, suppressed by Opinion 185] [Gastropoda].

FLEMINGOSTREINI Stenzel, 1971

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*, N3: 1150

Type genus: †*Flemingostrea* Vredenberg, 1916

FORDILLIDAE Pojeta, 1975 [14 June]

Reference: *Bulletins of American Paleontology*, 67(287): 366

Type genus: †*Fordilla* Barrande, 1881

Remarks: -oidea, Starobogatov (1977: 135).

FORTIPECTININAE Masuda, 1963 [10 December]

Reference: *Transactions and Proceedings of the Palaeontological Society of Japan*, new ser., 52: 149, 150

Type genus: *Fortipecten* Yabe & Hatai, 1940

FOSSULINI Bonetto, 1966 [31 March]

Reference: *Archiv für Molluskenkunde*, 95(1–2): 3

Type genus: *Fossula* I. Lea, 1870

FRAGILLIDAE S. V. Wood, 1874 [February]

Reference: *A monograph of the Crag Mollusca*, 3(2): 120

Remarks: Established as a family containing the genera *Lepton*, *Lasaea*, *Bornia*, *Scacchia*, *Scintilla*, *Kellia*, *Montacuta*, and *Sphenalia*. Not available: not based on a genus.

FRAGINAE Stewart, 1930 [9 August]

Reference: *The Academy of Natural Sciences of Philadelphia, Special Publication* 3: 271

Type genus: *Fragum* Röding, 1798

Remarks: -ini, Kafanov & Popov (1977: 59); -idae, Scarlato & Starobogatov (1979a: 23).

FREJIDAE Ratter & Cope, 1998 [September]

Reference: *Palaeontology*, 41(5): 976

Type genus: †*Freja* Liljedahl, 1984

FRENGUELLIELLINAE Nakano, 1960

Reference: *Journal of Science of the Hiroshima University*, ser. C, 3(2): 246

Type genus: †*Frenguelliella* A. F. Leanza, 1942

Remarks: -idae, M. R. Cooper (1991: 10).

FRIERSONIINAE Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 70, 287

Type genus: *Friersonia* Ortmann, 1912

FURCATIINI Waterhouse, 2001 [1 July]

Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 133

Type genus: †*Furcatia* Waterhouse, 2001

FURCELLINAE Bronn, 1862

Reference: *Die Klassen und Ordnungen der Weichthiere*, 3(2): 476, 503

Type genus: *Furcella* Lamarck, 1801

Remarks: Original spelling *Furcellana*, established as a "Sippe" immediately below family rank.

GAFRARIIDAE Korobkov, 1954

Reference: *Spravochnik i metodicheskoe rukovodstvo po tretrichnym molliuskam*: 166

Type genus: *Gafrarium* Röding, 1798

Remarks: Placed on the Official List by Opinion 1189 (1981: 244). -inae [declared new], F. Nordsieck (1969: 107).

GAIMARDIIDAE Hedley, 1916 [6 November]

Reference: *Australasian Antarctic Expedition 1911–1914, Scientific Reports*, ser. C, Zoology and Botany, 4(1): 26

Type genus: *Gaimardia* Gould, 1852

Remarks: Original spelling *Gaimardiadae*. -oidea [as -acea], Haas (1929: 17). Before Hedley, *Modiolarca* and *Modiolarcidae* were in current use, but Hedley correctly noticed that *Modiolarca* had been first established by Gray for *Mytilus impactus* Hermann, 1782, and therefore in a sense different from when Gray (1854a) established the family name

Modiolarcidae; as a consequence, Hedley replaced *Modiolarca* and Modiolarcidae with *Gaimardia* and Gaimardiidae. Art. 40.2 does not apply. See Modiolarcidae.

GALATHEAVALVIDAE Knudsen, 1970 [6 November]

Reference: *Galathea Report*, 11: 156

Type genus: *Galathea* Knudsen, 1970

GALEOMMATIDAE Gray, 1840b [16 October]

Reference: *Synopsis of the contents of the British Museum*, ed. 42: 150

Type genus: *Galeomma* Turton, 1825

Remarks: Original spelling Galeommidae. Established independently [as Galeomatidae] by F. Nordsieck (1969: 90). -inae [as -ana], Bronn (1862: 475, 500); -oidea, Nevesskaja et al. (1971: 16).

GARINAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b, 113

Type genus: *Gari* Schumacher, 1817

Remarks: -idae, Stewart (1930: 280).

GASTROCHAENIDAE Gray, 1840b [16 October]

Reference: *Synopsis of the contents of the British Museum*, ed. 42: 134, 150

Type genus: *Gastrochaena* Spengler, 1783

Remarks: Original spelling Gastrochaenadae. -inae [as -aina], Gray (1858b: 316); -oidea [as -acea], Haas (1929: 19). See also Chaeninae.

GELONIDAE Iredale, 1943 [30 April]

Reference: *The Australian Zoologist*, 10(2): 192

Type genus: *Geloina* Gray, 1842

Remarks: Established as a substitute name for Cyrenidae, based on *Cyrena*, earlier used as a valid name for taxa now placed in *Batissa* and *Geloina*; when *Cyrena* was placed in the synonymy of *Corbicula*, Iredale established Gelonidae because he considered that *Geloina* and *Batissa* belonged to a different family.

GEMMINAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 552

Type genus: *Gemma* Deshayes, 1853

Remarks: -idae [declared new], Frizzell (1936a: 415).

GIRTYPECTININAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 150

Type genus: †*Girtypecten* Newell, 1938

GLABARINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 175

Type genus: *Glabaris* Gray, 1847

Remarks: By First Reviser action, Parodiz & Bonetto (1963: 206) determined the precedence of the simultaneously published Anodontitinae over Glabarinae.

GLAUCOMYIDAE P. P. Carpenter, 1861

Reference: *Annual Report of the Board of Regents of the Smithsonian Institution for 1860*: 257

Type genus: *Glaucomya* S. P. Woodward, 1854

Remarks: -inae [as Glauconomyana], Bronn (1862: 476, 501).

GLAUCONOMIDAE Gray, 1853 [1 January]

Reference: *Annals and Magazine of Natural History*, ser. 2, 11(61): 37

Type genus: *Glaucnome* Gray, 1828

Remarks: Glauconomyidae [Chenu, 1862: 100] is an incorrect subsequent spelling. -oidea [as -iacea], Habe (1977: 277).

GLEBULINI Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 70, 287

Type genus: *Glebula* Conrad, 1853

GLOMINAE Verrill & Bush, 1897 [January]

Reference: *American Journal of Science*, 3: 53, 59

Type genus: *Glomus* Jeffreys, 1876

Remarks: -idae, Verrill & Bush (1898: 847).

Invalid: Type genus a junior homonym of *Glomus* Gistel, 1848; see Pristiglomidae.

GLOSSIDAE Gray, 1847 [November] (1840)

Reference: *Proceedings of the Zoological Society of London*, 15: 195

Type genus: *Glossus* Poli, 1795

Remarks: Gray did not give reasons for establishing the name Glossidae, but he treated *Isocardia* Lamarck, 1799, as a synonym of *Glossus*, and Glossidae can be considered a substitute name for Isocardiidae. Glossidae is in prevailing usage and it is conserved under Art. 40.2, with the priority of Isocardiidae (1840). -oidea [as -acea], Habe (1951: 115). See also Bucardiidae.

GLYCIMERIDAE Bronn, 1849

Reference: *Index Palaeontologicus*, Abt. 2. B, *Enumerator palaeontologicus*: 341

Type genus: *Glycimeris* Lamarck, 1799

Remarks: Original spelling (family) Glycimerina. First established as "Les Glycymerides" (vernacular) by Deshayes (1839: 124). Invalid: Type genus placed on the Official Index by Opinion 1414 (1986: 258).

GLYCYMERIDINAE Dall, 1908 (1847)

Reference: *Bulletin of the Museum of Comparative Zoology*, 43(6): 399

Type genus: *Glycymeris* da Costa, 1778

Remarks: Original spelling Glycymerinae. Placed on the Official List, with the spelling Glycymerididae, and attributed to Newton (1916), by Opinion 1414 (1986: 258). -idae, Newton (1916: 81, 83); -oidea, Nevesskaja et al. (1971: 14). When he established the name Glycymerinae, Dall did not cite Pectunculidae, but he listed *Pectunculus* Lamarck, 1799, in the synonymy of *Glycymeris* da Costa, 1778. Glycymerididae is in prevailing usage. It is maintained under Art. 40.2 with the priority of Pectunculidae (1847).

GLYPTARCIDAE Cope, 1996 [December]

Reference: *Palaeontology*, 39(4): 990, 991

Type genus: †*Glyptarca* Hicks, 1873

Remarks: -oidea, same reference.

GNATHODONTIDAE Neumayr, 1884

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, Abt. 1, 88(2): 408

Type genus: *Gnathodon* G. B. Sowerby I, 1832, ex Gray ms

Remarks: Original spelling "Gnathodontiden" (vernacular). Latinized by P. Fischer (1884: 118). Invalid: *Gnathodon* Oken, 1816 [Pisces], is not an available name (published in a work placed on the Official Index), but *Gnathodon* Goldfuss, 1820, is a senior homonym. See also Rangiidae.

GNESIOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 6

Type genus: †*Gnesioceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

GONIDEINAE Ortmann, 1916 [28 September]

Reference: *The Nautilus*, 30(5): 53

Type genus: *Gonidea* Conrad, 1857

Remarks: -ini, J. B. Burch (1975: 2).

GONIOCARDIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 23, 25

Type genus: †*Goniocardium* Vasseur, 1880

GONIOPHORINIDAE Sánchez, 2006 [30 March]

Reference: *Ameghiniana*, 43(1): 118

Type genus: †*Goniophorina* Isberg, 1934

GOULDIIDAE Stewart, 1930 [9 August]

Reference: *The Academy of Natural Sciences of Philadelphia, Special Publication* 3: 146

Type genus: *Gouldia* C.B. Adams, 1847

Remarks: -inae, Mikkelsen et al. (2006: 451, 495).

GRAMMATODONTIDAE Stephenson, 1941

Reference: *The University of Texas Publication*, 4101: 181

Type genus: †*Grammatodon* Meek & Hayden, 1860

Remarks: Name only, no description. Branson (1942: 249) treated *Parallelodon* as a subgenus of *Grammatodon*, and as a consequence substituted Parallelodontidae by Grammatodontidae. -inae, Newell (in Moore, ed., 1969: 257), who attributed the name to Branson.

GRAMMYSIIDAE S. A. Miller, 1877

Reference: *The American Palaeozoic fossils*: 180

Type genus: †*Grammysia* de Verneuil, 1847

Remarks: Original spelling Grammysidae. -oidea [as -acea], Dickins (1963: 41).

GROEBERELLIDAE Pérez, Reyes & Damborenea, 1995 [27 December]

Reference: *Revista Geologica de Chile*, 22(2): 147

Type genus: †*Groeberella* H. A. Leanza, 1993

GRUENEWALDIIDAE M. R. Cooper, 1991

Reference: *Annals of the South African Museum*, 100(1): 4

Type genus: †*Gruenewaldia* Wöhrmann, 1889

GRYPHAEINAE Vialov, 1936 [4 October]

Reference: *Doklady Akademii Nauk SSSR*, ser. 2, 4(1): 19

Type genus: †*Gryphaea* Lamarck, 1801
 Remarks: -idae, Stenzel (in Moore, ed., 1971: 1097); -oidea, Scarlato & Starobogatov (1979a: 21). Placed on the Official List by Opinion 356 (1955: 105), where it was attributed to Vialov (1937: 1631).

GRYPHAEOSTREINI Stenzel, 1971
 Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*, N3: 1125
 Type genus: †*Gryphaeostrea* Conrad, 1865
 Remarks: -idae, Sobetskij (1982: 135); -inae, Freneix (1982: 230).

GUANGXICONCHIDAE Zhang, 1999 [October]
 Reference: *Professional Papers of Stratigraphy and Palaeontology*, 27: 151 [Chinese text], 163 [English text]
 Type genus: †*Guangxiconcha* Zhang, 1977

GUIZHOUPECTININAE Astafieva, 1994
 Reference: *Paleontological Journal*, 28(1A): 15
 Type genus: †*Guizhoupecten* Chen, 1962

GYROPLEURIDAE MacGillavry, 1935
 Reference: *Koninklijke Akademie van Wetenschappen te Amsterdam. Proceedings of the Section of Sciences*, 38(5): 560
 Type genus: †*Gyropleura* Douvillé, 1887
 Remarks: Latinisation of the vernacular "Gyropleuridés", "/-inés", by Paquier (1905: 50, unavailable vernacular name introduced after 1900).

HAENLEINIINAE Heinz, 1932
 Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 12
 Type genus: †*Haenleinia* Böhm, 1907
 Remarks: Original spelling Haenleininae. Name only, no description. Not available unless discovery of an author who used the name as valid before 2000.

HALOBIIDAE Kittl, 1912
 Reference: *Resultate der Wissenschaftlichen Erforschung des Balatonsees*, 1(1), *Anhang. Palaeontologie der Umgebung des Balatonsees*, 2(4): 5
 Type genus: †*Halobia* Bronn, 1830
 Remarks: -inae, Ichikawa (1958: 189); -oidea, H. J. Campbell (1994: 64).

HALONYMPHIDAE Scarlato & Starobogatov, 1983
 Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 13

Type genus: *Halonympha* Dall & E. A. Smith, 1886

HAWAIARCAINAE Noda, 1986
 Reference: *Palaeontological Society of Japan, Special Paper*, 29: 58, 59
 Type genus: *Hawaiarca* Dall, Bartsch & Rehder, 1938

HAYASAKAPECTINIDAE Boyd & Newell, 2000 [October]
 Reference: *Acta Palaeontologica Sinica*, 39(4): 533
 Type genus: †*Hayasakapecten* Nakazawa & Newell, 1968
 Remarks: -inae, Carter, herein.

HEALEYIDAE Hautmann, 2008 [May]
 Reference: *Journal of Paleontology*, 82(3): 562
 Type genus: †*Healeyia* Hautmann, 2001

HELIGMINAE. See Eligminae.

HELIOCERAMINAE Heinz, 1932
 Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 19
 Type genus: †*Helioceramus* Heinz, 1932
 Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

HEMIDONACIDAE Scarlato & Starobogatov, 1971 [before 7 July]
 Reference: [in Nevesskaia et al.] *Paleontologicheskii Zhurnal*, 1971(2): 16
 Type genus: *Hemidonax* Mörch, 1870
 Remarks: Published almost simultaneously by Boss (1971 [20 July]: 9). Not available (no description) from Iredale & McMichael (1962: 21). -ini, Kafanov & Popov (1977: 60).

HEMIPLECTININAE Habe, 1977
 Reference: *Systematics of Mollusca in Japan (Bivalvia and Scaphopoda)*: 88
 Type genus: *Hemipecten* A. Adams & Reeve, 1849
 Remarks: Original spelling Hemipectinae.

HEMISOLASMINAE Starobogatov, 1970
 Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 73, 192
 Type genus: *Hemisolasma* Rafinesque, 1831
 Remarks: Declared nom. nov. pro Diplasminae Modell, 1942, but no justification given.

HETERANOMIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 21, 31

Type genus: *Heteranomia* Winckworth, 1922

Remarks: -oidea, same reference.

HETEROCAPRINIDAE Munier-Chalmas, 1873 [31 January]

Reference: *Journal de Conchyliologie*, 21(1): 73

Type genus: †*Heterocaprina* Munier-Chalmas, 1873

HETERODICERATIDAE Pchelintsev, 1959

Reference: *Rudisty Mezozoya Gornogo Kryma*: 80

Type genus: †*Heterodicerias* Hébert, 1870

Remarks: -inae, Coogan (in Moore, ed., 1969: 778).

HETEROPECTININAE Beurlen, 1954 [19 December]

Reference: *Paleontologia do Parana*: 113

Type genus: †*Heteropecten* Kegel & da Costa, 1951

Remarks: Independently declared new by Waterhouse (2008: 143).

HETEROPERIA Rafinesque, 1815

Reference: *Analyse de la nature*: 146

Remarks: Established as a subfamily of Veneridae containing the genera *Venericardia*, *Meretrix*, *Venus*, *Cardita*, *Paphia*, etc. Not available as a family-group name (not based on a genus).

HETEROTRIGONIINI M. R. Cooper, 1991

Reference: *Annals of the South African Museum*, 100(1): 26

Type genus: †*Heterotrigonia* Cox, 1952

HEUDEANINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 184

Type genus: *Heudeana* Frierson, 1922

Remarks: -ini, Starobogatov (1970: 60).

HIATELLIDAE Gray, 1824

Reference: *A supplement to the Appendix of Captain Parry's voyage for the discovery of a north west passage ...*, Appendix: ccxli

Type genus: *Hiatella* Bosc, 1801

Remarks: Original spelling Hyatelladae, based on *Hyatella*, an incorrect subsequent spelling of *Hiatella*. -oidea [as -acea, in synonymy of Saxicavoidea], Eberzin (1960: 133).

HINNITINAE Habe, 1977

Reference: *Systematics of Mollusca in Japan (Bivalvia and Scaphopoda)*: 87

Type genus: †*Hinnites* Defrance, 1821

Remarks: -ini, Vaught (1989: 119).

HIPPOCARDIIDAE Pojeta & Runnegar, 1976

Reference: *United States Geological Survey Professional Paper*, 968: 74

Type genus: †*Hippocardia* T. Brown, 1843

Remarks: Established as a family of Rostroconchia. Classified in the bivalve superorder Septibranchia by Starobogatov (1977), an opinion not followed by later authors.

HIPPOMYIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 20, 28

Type genus: †*Hippomya* Salter, 1864

HIPPOPODIUMIDAE Cox, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 582

Type genus: †*Hippopodium* J. Sowerby, 1819

Remarks: Not available (no description) from Cox (1965: 82). Original spelling Hippopodidae. Placed on the Official List and spelling emended to Hippopodiumidae by Opinion 2036 (2003: 157, 158).

HIPPURITELLINAE Bilotte, 1982

Reference: *Bulletin de la Société d'Histoire Naturelle de Toulouse*, 117: 111

Type genus: †*Hippuritella* Douvillé, 1908

HIPPURITIDAE Gray, 1848 [1 December]

Reference: *Annals and Magazine of Natural History*, ser. 2, 2(12): 440

Type genus: †*Hippurites* Lamarck, 1801

Remarks: Established by d'Orbigny (1842: 176), as "Hippuridées", but family name not generally attributed to that author. Placed on the Official List by Opinion 613 (1961: 355). -inae, MacGillavry (1935: 560); -oidea [as -acea], Newell (1965: 19).

HOCHSTETTERIIDAE Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 304

Type genus: *Hochstetteria* Vélain, 1877

Remarks: Name only, no description. Not available, unless discovery of an author who used the name as valid before 2000.

HOLDHAUSIELLINAE Beurlen, 1954 [19 December]

Reference: *Paleontologia do Parana*: 123

Type genus: †*Holdhausiella* Mendes, 1952

HORIOPLEURIDAE Yanin, 1990

Reference: [in Menner, ed.] *Sistematika i filogeniia bespozvonochnykh. Kriterii vydeleniia vychikh taksonov*: 65

Type genus: †*Horiopleura* Douvillé, 1889

HUMPHREYIIDAE Gray, 1858a [1 July]

Reference: *Annals and Magazine of Natural History*, ser. 3, 2(1): 18

Type genus: *Humphreyia* Gray, 1858

Remarks: Original spelling Humphreyiadae. Independently declared new by Scarlato & Starobogatov (1979a: 22, 32).

HUNANOPECTINIDAE Yin, 1985 [November]

Reference: [Yin Hong-fu] *Acta Palaeontologica Sinica*, 24(6): 636 [Chinese], 638 [English abstract]

Type genus: †*Hunanopecten* Zhang, 1977

Remarks: Independently declared new by Fang (1987: 376 [Chinese], 404 [English]). -inae / -ini, Waterhouse (2001: 133).

HUXLEYIIDAE Scarlato & Starobogatov, 1971

Reference: [in Nevesskaja et al.] *Paleontologicheskii Zhurnal*, 1971(2): 12

Type genus: *Huxleyia* A. Adams, 1860

Remarks: Original spelling Huxleyidae. -oidea, same reference.

HYOTISSINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 23

Type genus: *Hyotissa* Stenzel, 1971

Remarks: Original spelling Hiotissinae. -ini [declared new], Harry (1985: 130).

HYPANINAE Starobogatov, 1970 [after 15 October]

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 87

Type genus: *Hypanis* Ménétries, 1832

Remarks: Introduced, in violation of Art. 40.1, as a nom. nov. pro Adacninae, based on *Adacna* Eichwald, 1838 (by Starobogatov ranked as a subgenus of *Hypanis*). -ini, Kafanov & Popov (1977: 61).

HYPOGAEIDAE Rafinesque, 1815

Reference: *Analyse de la nature*: 146

Type genus: *Hypogaea* Poli, 1791

Remarks: Original spelling Hypogidia, containing *Pholas* and 14 other genera. The name *Hypogaea* Poli, 1791 is not cited by Rafinesque, but is a synonym of *Pholas*.

Alternatively, "Hypogidia" might also be regarded as a descriptive term, meaning "living underground", in which case Hypogaeidae would not be an available name. We choose the first alternative, as there are no negative nomenclatural consequences, Hypogaeidae being a junior synonym of Pholadidae.

HYRCANIINI Kafanov & Starobogatov, 1977

Reference: [in Kafanov & Popov] *Paleontologicheskii Zhurnal*, 1977(3): 63

Type genus: †*Hyrkania* Kolesnikov, 1950

Remarks: Invalid: type genus a junior homonym of *Hyrkania* Monterosato, 1894 [Gastropoda].

HYRIDELLINAE McMichael & Hiscock, 1958 [1 October] (1934)

Reference: *Australian Journal of Marine and Freshwater Research*, 9(3): 435

Type genus: *Hyridella* Swainson, 1840

Remarks: Name attributed by the authors to Iredale. McMichael & Hiscock treated *Propehyridella* as a synonym of *Hyridella*, and introduced Hyridellinae as a replacement for Propehyridellinae; Hyridellinae is in prevailing usage and it is maintained under Art. 40.2 with the priority of Propehyridellinae (1934). -idae, Purchon (1958 [December]: 492); -ini, Starobogatov (1970: 72).

HYRIINAE Swainson, 1840 [May]

Reference: *A treatise on malacology*: 266, 268, 379

Type genus: *Hyria* Lamarck, 1819

Remarks: Original spellings Hyrinae and Hyrianae. -idae, Nevesskaja et al. (1971: 13); -ini, Graf & Cummings (2006: 394); -oidea, Bogan, Campbell, Hartmann & Hoeh, herein (pers. com.).

HYRIOPSINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 188

Type genus: *Hyriopsis* Conrad, 1853

Remarks: Independently declared new by Habe (1977: 116).

ICANOTIIDAE Casey, 1961 [9 March]

Reference: *Palaeontology*, 3(4): 581

Type genus: †*Icanotia* Stoliczka, 1870

ICHTHYOSARCOLITINI Douvillé, 1887 (1871)

Reference: *Bulletin de la Société Géologique de France*, ser. 3, 15: 759, 791

Type genus: †*Ichthyosarcolites* Desmarest, 1812

Remarks: Original spelling (tribe) “Ichthyosarcolitínés” (vernacular). First latinized (as Ichthyosarcolitinae) by MacGillavry (1937: 46), without reference to Douvillé. -idae, Skelton (1978: 316); -oidea, Yanin (1990: 67), who both attributed the name to Douvillé. *Ichthyosarcolites* is a senior objective synonym of *Caprinella*, and under Art. 40.2 Ichthyosarcolitidae is conserved over Caprinellidae with the priority of the latter (1871).

IDONEARCIDAE Scarlato & Starobogatov, 1979
Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25
Type genus: †*Idonearca* Conrad, 1862

ILIONIIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*, 80: 22
Type genus: †*Ilionia* Billings, 1875
Remarks: Original spelling Illioniidae, based on *Illionia*, an incorrect subsequent spelling of *Ilionia*. -inae, J. D. Taylor, herein (pers. com.).

INOCERAMIDAE Giebel, 1852
Reference: *Allgemeine Palaeontologie, Abt. 1, Palaeozoologie*, ed. 2: 64, 166
Type genus: †*Inoceramus* J. Sowerby, 1814
Remarks: Placed on the Official List by Opinion 473 (1957: 281), but attributed in error to Zittel (1881). -inae, Zittel (1881: 36); -oidea, Nevesskaja et al. (1971: 15).

INTIHUARELLIDAE Sánchez, 2003 [30 September]
Reference: [in Sánchez & Vaccari] *Ameghiniana*, 40(3): 418
Type genus: †*Intihuarella* Sánchez, 2003

IOTRIGONIINAE Saveliev, 1958
Reference: *Trudy Vsesoiuznogo Neftianogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Instituta [VNIGRI]*, 125: 108
Type genus: †*Iotrigonia* van Hoepen, 1929
Remarks: -idae, M. R. Cooper (1991: 43).

IRIDININAE Swainson, 1840 [May]
Reference: *A treatise on malacology*: 266, 268, 380
Type genus: *Iridina* Lamarck, 1819
Remarks: Original spellings Iridinae and Iridini-nae. -idae, Gray (1840b [16 October]: 142, 150). Subfamily independently declared new by Modell (1942: 176).

ISCHYRINIINAE Kobayashi, 1933
Reference: *Journal of the Faculty of Science, Imperial University of Tokyo, section 2*, 3(7): 298, 316
Type genus: †*Ischyrinia* Billings, 1866
Remarks: Original spelling Ischyrinae. -idae, Pojeta & Runnegar (1976: 62); -oidea, Starobogatov (1977: 138). Established as a family of bivalves, but now included in the separate class Rostroconchia.

ISCHYRODONTIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*, 80: 20, 26
Type genus: †*Ischyrodonta* Ulrich, 1890

ISOARCIDAE Keen, 1969
Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 241
Type genus: †*Isarca* Münster, 1842

ISOCARDIIDAE Gray, 1840b [16 October]
Reference: *Synopsis of the contents of the British Museum*, ed. 42: 137, 150
Type genus: *Isocardia* Lamarck, 1799
Remarks: Original spelling Isocardiadae. Established independently by Bucquoy, Dautzenberg & Dollfus (1892: 313). -inae [as -ana], Bronn (1862: 475, 500); -oidea [as -acea], Dall (1895a: 550). See Glossidae.

ISOCYPRINIDAE R. N. Gardner, 2005 [June]
Reference: *New Zealand Journal of Geology and Geophysics*, 48(2): 356
Type genus: †*Isocyprina* Roeder, 1882

ISODONTIDAE Arkell, 1934 [December]
Reference: *A monograph of British corallian Lamellibranchia*: 309
Type genus: †*Isodonta* Buvignier, 1851
Remarks: Name only, no description. Arkell did not give explanations for his establishing the name Isodontidae, but he explained why he [erroneously, in our opinion] considered Sowerbya d'Orbigny, 1850, unavailable and *Isodonta* the valid name, and he probably intended Isodontidae as a substitute name for Sowerbyidae Cox, 1929. Isodontidae is not in prevailing usage and Art. 40.2 does not apply.

ISOGNOMONIDAE Woodring, 1925 (1828)
Reference: *Carnegie Institution of Washington, Publication*, 366: 57

Type genus: *Isognomon* Lightfoot, 1786

Remarks: When he established the name Isognomonidae, Woodring did not cite Pernidae or Melinidae, but he cited *Perna* and *Melina* as synonyms of *Isognomon*. Isognomonidae is in prevailing usage, and it is conserved under Art. 40.2 with the priority of Pernidae (1828). -inae, Eberzin (1960: 80); -oidea, Nevesskaja (2003: 617).

ISOLIMEIDAE Kasum-Zade, 2003

Reference: [Advance in research of Mesozoic bivalve mollusks in Azerbaijan Order Pectinoida: revision and systematics]: 61, 87

Type genus: *Isolimea* Iredale, 1929

Remarks: Original spelling Isolimidae.

ISOPERIA Rafinesque, 1815

Reference: *Analyse de la nature*: 146

Remarks: Established as a subfamily of Veneridae containing the genera *Ungulina*, *Lucina*, *Cyclas*, *Tellina*, *Cerastes* and *Isocardia*. Not available as a family-group name (not based on a genus).

JANACEKIIDAE Růžicka & Řehoř, 1978

Reference: [in Hajkr et al.] *Freiberger Forschungshefte*, ser. C (Geowissenschaften-Paläontologie), 325: 37

Type genus: †*Janacekia* Růžicka & Řehoř, 1978

Remarks: Combined family and genus description.

JILINOCONCHIDAE Ma, 1989

Reference: *Symposium on the Cretaceous of Southern China*: 259

Type genus: †*Jilinoconcha* Ma, 1989

Remarks: Original spelling Jilinoconchadidae.

JOLYIDAE Bourguignat, 1880 [May]

Reference: *Matériaux pour servir à l'histoire des Mollusques acéphales du système européen*: 5

Type genus: *Jolya* Bourguignat, 1877

Remarks: Original spelling Jolydae. Under Art. 23.9 of the Code, Jolyidae Bourguignat, 1880, is here declared a *nomen oblitum* and Modiolidae G. Termier & H. Termier, 1950, a *nomen protectum*: see under Modiolidae.

JOUANNETIINAE Tryon, 1862 [before 1 August]

Reference: *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14: 193, 194

Type genus: †*Jouannetia* Desmoulins, 1828

Remarks: Original spelling Jouannetinae. See also Martesiinae.

JOUIINAE Karacabey-Oztemür, 1981 [August]

Reference: *Bulletin of the Mineral Research and Exploration Institute of Turkey*, 92: 44

Type genus: †*Joufia* Boehm, 1897

JULIIDAE E. A. Smith, 1885 [after September]

Reference: *Report on the scientific results of the voyage of H. M. S. Challenger, Zoology*, 13(1): 269

Type genus: *Julia* Gould, 1862

Remarks: Established as a family of bivalves, but now classified as gastropods (see Bouchet & Rocroi, 2005: 260).

KALENTERIDAE Marwick, 1953

Reference: *New Zealand Geological Survey, Paleontological Bulletin*, 21: 69

Type genus: †*Kalentera* Marwick, 1953

Remarks: -oidea, Nevesskaja et al. (1971: 17).

KELLIELLIDAE P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (11): 1022

Type genus: *Kelliella* M. Sars, 1870

Remarks: Original spelling Kellyellidae, based on *Kellyella* P. Fischer, 1887, an unjustified emendation of *Kelliella*. -oidea, Nevesskaja et al. (1971: 18).

KELLIIDAE Forbes & Hanley, 1849 [1 January]

Reference: *A history of British Mollusca and their shells*, 2(13): 14

Type genus: *Kellia* Turton, 1822

Remarks: Original spelling Kelliadae. -inae [declared new], F. Nordsieck (1969: 86), and independently declared new by F. R. Bernard (1983: 30, 68); -oidea, Nevesskaja et al. (1971: 16).

KIJIDAE Kolesnikov, 1977

Reference: *Paleontologicheskii Zhurnal*, 1977(3): 50

Type genus: †*Kija* Lebedew, 1958

KINERKAELLIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 28

Type genus: †*Kinerkaella* Khalfin, 1950

Remarks: Not available (no description) from Betekhtina (1972: 65), nor from Betekhtina (1974: 126).

KITSONIIDAE Eames, 1957 [October]

Reference: *Bulletin of the British Museum (Natural History)*, *Geology*, 3(2): 68

Type genus: †*Kitsonia* Eames, 1957

KOCHIINAE Frech, 1891

Reference: *Abhandlungen zur Geologischen Spezialkarte von Preussen und den Thüringischen Staaten*, 9(3): 332 [72]

Type genus: †*Kochia* Frech, 1891

Remarks: Independently declared new by Mailieux (1920: 149). -idae, Maillieux (1931: 62, 69).

KOLYMIIDAE Kuznetsov, 1973

Reference: *Novosti Geologii iakutii*, 3: 23

Type genus: †*Kolymia* Likharev, 1941

Remarks: -inae, Biakov (2008: 18).

KONDURIIDAE Sánchez, 2007 [August]

Reference: [in Sánchez & Benedetto] *Geobios*, 40(4): 530

Type genus: †*Konduria* Sánchez, 2007

KUPHINAE Tryon, 1862 [before 1 August]

Reference: *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14: 193, 194

Type genus: *Kuphus* Guettard, 1770

KYMATOXINAE Stenzel & Krause, 1957

Reference: [in Stenzel, Krause & Twining] *The University of Texas, Bureau of Economic Geology, Publication*, 5704: 124

Type genus: †*Kymatox* Stenzel & Krause, 1957

Remarks: Combined description of family- and genus-group names.

LACUSTRININAE Korniushev, 1989

Reference: *Zoologicheskii Zhurnal*, 68(11): 22

Type genus: *Lacustrina* Sterki, 1916

LAEVICARDIINAE Keen, 1951 [July]

Reference: *Minutes, Conchological Club of Southern California*, 111: 7

Type genus: *Laevicardium* Swainson, 1840

Remarks: First published, without a description by Keen (1936: 367), but rejected under Art. 13(a)(i) of the 3rd edition of the Code by Vidal (1994: 95). -ini, Kafanov & Popov (1977: 59).

LAEVITRIGONIINAE Saveliev, 1958

Reference: *Trudy Vsesoiuznogo Neftianogo Nauchno-Issledovatel'skogo Geologorazvedchnogo Instituta [VNIGRI]*, 125: 110

Type genus: †*Laevitrigonia* Lebküchner, 1932

LAHILLIINAE Finlay & Marwick, 1937 [20 May]

Reference: *New Zealand Geological Survey, Palaeontological Bulletin*, 15: 30

Type genus: †*Lahillia* Cossmann, 1899

Remarks: -idae, Marwick (1944: 255).

LAMELLIDENTINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 188

Type genus: *Lamellidens* Simpson, 1900

LAMELLODONTIDAE Vogel, 1962

Reference: *Akademie der Wissenschaften und der Literatur in Mainz, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse*, 1962(4): 216

Type genus: †*Lamellodonta* Vogel, 1962

Remarks: -oidea, Nevesskaja et al. (1971: 13). Established as a bivalve, but demonstrated by Havlicek & Kříž (1978: 972) to be a brachiopod.

LAMELLOTIDAE Horvath, 1966

Reference: *Földtani Közlöny*, 96(1): 106 [Hungarian text], 110 [German text]

Type genus: †*Lamellotis* Horvath, 1966

Remarks: -oidea [as -acea], H. A. Vokes (1980: 232).

LAMETILIDAE Allen & Sanders, 1973 [July]

Reference: *Bulletin of the Museum of Comparative Zoology*, 145(6): 287

Type genus: *Lametila* Allen & Sanders, 1973

LAMNIPLECTININAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 157

Type genus: †*Lamnipecten* Waterhouse, 2008

LAMPROTULINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 187

Type genus: *Lamprotula* Simpson, 1900

LAMPSILINAE Ihering, 1901 [3 September]

Reference: *The Nautilus*, 15(5): 53

Type genus: *Lampsilis* Rafinesque, 1820

Remarks: Name attributed to himself by Ortmann (1911a: 337). -idae, Hannibal (1912: 119); -ini, Starobogatov (1970: 68, 71).

LAPEIROUSIINAE Kühn, 1932 [June]

Reference: *Records of the Geological Survey of India*, 66(1): 164

Type genus: †*Lapeirousia* Bayle, 1878

Remarks: Original spelling *Lapeirouseiinae*, based on *Lapeirouseia*, an incorrect subse-

quent spelling of *Lapeirousia*. -oidea / -idae, Yanin (1990: 67).

LASAEIDAE Gray, 1842 [21 May]

Reference: *Synopsis of the contents of the British Museum*, ed. 44: 79, 91

Type genus: *Lasaea* Brown, 1827

Remarks: Original spelling Lasiadae. -inae [as Laseana, based on *Lasea*, an incorrect subsequent spelling of *Lasaea*], Bronn (1862: 475, 500).

LATERNULIDAE Hedley, 1918 [19 June] (1840)

Reference: *Journal and Proceedings of the Royal Society of New South Wales*, 51, supplement: M12

Type genus: *Laternula* Röding, 1798

Remarks: -oidea [as -acea], Cotton & Godfrey (1938: 130); -inae, Korobkov (1954: 209). When he established Laternulidae, Hedley did not cite Anatinidae, but he implicitly treated *Anatina* Lamarck, 1818, as a synonym of *Laternula*, and Laternulidae takes the priority of Anatinidae under Art. 40.2.

LAURSKIIDAE Khalfin, 1948

Reference: *Izvestiia Tomskogo Politekhnicheskogo Instituta*, 65(1): 229

Type genus: †*Laurskia* Khalfin, 1948

LAVIGNONIDAE Récluz, 1869

Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): 6, and unnumbered table between pp. 34 and 35

Type genus: *Lavignonus* Férussac, 1822

LEDELLINAE Allen & Sanders, 1982 [12 January]

Reference: *Bulletin of the Museum of Comparative Zoology*, 150(1): 2

Type genus: *Ledella* Verrill & Bush, 1897

Remarks: Not available (no description) from Allen (1978: 392, as Ledellidae). -idae, Filatova & Schileyko (1985: 77); -oidea, Schileyko (1989: 94).

LEDIDAE Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 411

Type genus: *Leda* Schumacher, 1817

Remarks: Original spelling Ledadae. -inae, H. & A. Adams (1858: 546). See Nuculanidae.

LEGUMINAIINI Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 61, 283

Type genus: *Leguminaia* Conrad, 1865

LEILINAE Morretes, 1949

Reference: *Arquivos do Museu Paranense*, 7: 28

Type genus: *Leila* Gray, 1840

Remarks: Name only, no description. First diagnosed by Parodiz & Bonetto (1963: 206), who attributed the name to Morretes.

LEIOPECTINIDAE Krasilova, 1959

Reference: *Paleontologicheskii Zhurnal*, 1959(3): 42

Type genus: †*Leiopecten* Khalfin, 1940

Remarks: -oidea, Scarlato & Starobogatov (1979a: 21).

LEIOPTERIINAE Maillieux, 1920

Reference: *Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie*, 29: 150

Type genus: †*Leiopteria* Hall, 1883

Remarks: Original spelling Leiopterinae. -idae, Maillieux (1931: 64).

LENTIDIINAE H. A. Vokes, 1945 [10 October]

Reference: *Bulletin of the American Museum of Natural History*, 86: 6, 23

Type genus: *Lentidium* de Cristofori & Jan, 1832

LEPTOCHONDRIIDAE Newell & Boyd, 1995 [13 December]

Reference: *Bulletin of the American Museum of Natural History*, 227: 69

Type genus: †*Leptochondria* Bittner, 1891

Remarks: -inae, Waterhouse (2001: 116).

LEPTODESMATINAE Maillieux, 1931 [31 December]

Reference: *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 51: 70

Type genus: †*Leptodesma* Hall, 1883

Remarks: Original spelling Leptodesminae.

LEPTONIDAE Gray, 1847 [November]

Reference: *Proceedings of the Zoological Society of London*, 15: 193

Type genus: *Lepton* Turton, 1822

Remarks: -inae [as Leptana], Bronn (1862: 475, 500); -oidea [as -acea], Dall (1895a: 546).

LIAONINGIIDAE Yu & Dong, 1993

Reference: *Late Triassic stratigraphy and paleogeography of the northern part of the circum-Pacific belt. China*: 178

Type genus: †*Liaoningia* Yu & Dong, 1993

Remarks: Invalid: type genus a junior homonym of *Liaoningia* Xing & Liu, 1979 [Cnidaria].

LIBITINIDAE Thiele, 1926Reference: *Handbuch der Zoologie*, 5(3): 192Type genus: *Libitina* Schumacher, 1817

Remarks: Thiele did not give reasons for establishing the name Libitinidae, but he cited "*Trapezium* Megerle von Mühlfeld 1811 (non Mus. Calonn. 1797)" and *Cypricardia* Lamarck, 1819, in synonymy of *Libitina*, and he probably intended Libitinidae as a substitute name for Trapezidae and Cypricardiidae. However, contrary to Thiele's opinion, *Trapezium* is a valid name; Libitinidae is not in prevailing usage and Art. 40.2 does not apply. -oidea [as -acea], Korobkov (1954: 149).

LIMARCIDAE Scarlato & Starobogatov, 1979Reference: *Trudy Zoologicheskogo Instituta*, 80: 21, 29Type genus: †*Limarca* Tate, 1886

Remarks: -oidea, same reference.

LIMARIINAE

See Limidae.

LIMATULIDAE Kasum-Zade, 2003

Reference: [Advance in research of Mesozoic bivalve mollusks in Azerbaijan Order Pectinoida: revision and systematics]: 62, 88

Type genus: *Limatula* S. V. Wood, 1839

Remarks: -inae, Bieler, herein.

LIMATULININAE Waterhouse, 2001 [1 July]Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 128Type genus: †*Limatulina* de Koninck, 1885

Remarks: -idae, Waterhouse (2008: 132).

LIMINAE Rafinesque, 1815Reference: *Analyse de la nature*: 147Type genus: *Lima* Bruguière, 1797

Remarks: Original spelling (subfamily) Limaridia, based on *Limaria* Rafinesque, 1815, an unjustified emendation of *Lima* Bruguière, 1797 (and a junior homonym of *Limaria* Link, 1807). Under Art. 35.4.1, the name is to be corrected to Liminae. -idae, d'Orbigny (1846: 651; the first instance of the family-group name explicitly based on *Lima* Bruguière, 1797); -oidea [as -acea], Newell (in Moore, ed., 1969: 385).

LIMIPECTININAE Newell & Boyd, 1990 [26 April]Reference: *American Museum Novitates*, 2970: 4Type genus: †*Limipecten* Girty, 1904

Remarks: -idae, Waterhouse (2008: 151).

LIMNOCONCHAE Blainville, 1824Reference: *Dictionnaire des Sciences Naturelles*, 32: 323

Remarks: Original spelling "Les Limnoconques" (vernacular); latinized by Herrmannsen (1847: 605). Established as a division of the family Submytilacea, including the genera *Anodonta* and *Unio*. Not available as a family-group name (not based on a genus).

LIMNOCYRENIDAE Kolesnikov, 1977Reference: *Paleontologicheskii Zhurnal*, 1977(3): 50Type genus: †*Limnocyrena* Martinson, 1961**LIMNOPAPPIINAE** Schlickum, 1962 [30 June]Reference: *Archiv für Molluskenkunde*, 91(1–3): 110Type genus: †*Limnopappia* Schlickum, 1962

Remarks: -ini, Kafanov & Popov (1977: 60).

LIMNOPERNINAE Scarlato & Starobogatov, 1979Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25Type genus: *Limnoperma* Rochebrune, 1882**LIMNOSCAPHINAE** Lindholm, 1932Reference: *Trudy Vsesoiuznogo Geologo-Razvedochnogo Obedineniia Narodnyi Komissariat Tiazheloi Promyshlennosti [NKTP] SSSR*, 239: 12Type genus: †*Limnoscapha* Lindholm, 1932

Remarks: -ini, Bogatov & Zatravkin (1988: 158).

LIMOPSIDAE Dall, 1895 [March]Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 517Type genus: *Limopsis* Sassi, 1827

Remarks: -oidea [as -acea], Newell (1965: 17).

LIMOPTERINAE Maillieux, 1931 [31 December]Reference: *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 51: 72Type genus: †*Limoptera* Hall, 1869**LINOTRIGONIINAE** Yanin, 2004Reference: *Paleontological Journal*, 38, suppl. 6: 629Type genus: †*Linotrigonia* van Hoepen, 1929**LIOCONCHINAE** Habe, 1977Reference: *Systematics of Mollusca in Japan (Bivalvia and Scaphopoda)*: 258Type genus: *Lioconcha* Mörch, 1853

Remarks: Not available (no description) from Iredale & McMichael (1962: 22, as -idae).

LIOSTREINAE Vialov, 1983

Reference: *Doklady Akademii Nauk Ukrainskoi SSR*, ser. B, 11: 7

Type genus: †*Liostrea* Douvillé, 1904

Remarks: -inae [independently declared new] / -ini, Malchus (1990: 150).

LIPANELLIDAE Sánchez, 2005 [May]

Reference: *Journal of Paleontology*, 79(3): 538

Type genus: †*Lipanella* Sánchez, 2005

LITHARCINAE Frizzell, 1946 [29 January]

Reference: *Journal of Paleontology*, 20(1): 44

Type genus: *Litharca* Gray, 1842

Remarks: -idae [declared new], Scarlato & Starobogatov (1979b: 23).

LITHIOTIDAE Cox, 1971

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 1199

Type genus: †*Lithiotis* Gümbel, 1874

Remarks: Not available (vernacular name introduced after 1900) from “Lithiotiden” of Reis (1903: 2). -oidea [as -acea], Benini & Loriga (1977: 37).

LITHODOMINAE Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 417

Type genus: *Lithodomus* Cuvier, 1817

Remarks: Original spelling Lithodolina. See Lithophaginae.

LITHOPHAGELLIDAE Cossmann, 1911 [25 October]

Reference: [in Cossmann & Peyrot] *Actes de la Société Linnéenne de Bordeaux*, 65(2): 78

Type genus: *Lithophagella* Gray, 1854

Remarks: Cossmann treated *Lithophagella* as a synonym of *Coralliophaga* Blainville, 1824, and Lithophagellidae is not available under Art. 11.7.1.1.

LITHOPHAGINAE H. Adams & A. Adams, 1857 [December] (1854)

Reference: *The Genera of Recent Mollusca*, 2: 518

Type genus: *Lithophaga* Röding, 1798

Remarks: Lamarck (1812: 108; 1818: 423, 499) used the vernacular name “Les Lithophages” and this was latinized [as Lithophagi] by Bowdich (1822: 3, 4), [as Lithophaga] by Children (1823: 302), and [as Lithophagidae] by Broderip (1839: 319). However, this is a descriptive term (meaning

rock borers) to include the genera *Saxicava*, *Petricola* and *Venerupis*. Lithophagidae is not available from Lamarck or the latinizations of Lamarck. When they established Lithophaginae, H. & A. Adams did not refer to Lithodominæ, but *Lithophaga* Röding, 1798, and *Lithodomus* Cuvier, 1817, are objective synonyms; Lithophaginae is in prevailing usage, and is conserved under Art. 40.2 with the priority of Lithodominæ (1854).

LOPATINIIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25

Type genus: †*Lopatinia* Schmidt, 1872

LOPHINAE Vialov, 1936 [4 October]

Reference: *Doklady Akademii Nauk SSSR*, ser. 2, 4(1): 19

Type genus: *Lopha* Röding, 1798

Remarks: -idae, Sobetski (1982: 137); -ini, Harry (1985: 135).

LORTIELLINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 178

Type genus: *Lortiella* Modell, 1942

Remarks: Not available from Iredale (1934: 58, 77): type genus then not an available name (no type species designated).

LUCINIDAE J. Fleming, 1828 [March]

Reference: *A history of British animals*: 441, 442

Type genus: *Lucina* Bruguière, 1797

Remarks: Original spelling Lucinadae. -inae [as -ana], Bronn (1862: 475, 500); -oidea [as -acea], Gill (1871: 20) [Chavan (in Moore, ed., 1969: 491) attributed the subfamily rank to Anton (1838: xii, 6). Anton did use the spelling Lucinacea, without rank, immediately above genus; the context indicates that family rank was meant].

LUNARCIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24

Type genus: *Lunarca* Gray, 1842

LUNULACARDIIDAE P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (11): 1040

Type genus: †*Lunulacardium* Münster, 1840

Remarks: Original spelling Lunulicardiidae, based on *Lunulicardium*, an incorrect subsequent spelling of *Lunulacardium*. -oidea, Scarlato & Starobogatov (1979a: 20).

LUTETIIDAE Zhgenti, 1976

Reference: *Liutetsiidy srednego miotsena. Ikh evoliutsiia i stratigraficheskoe znachenie*: 15–17

Type genus: †*Lutetia* Deshayes, 1858

Remarks: Name attributed by Zhgenti to Davidaschvili (1970), who used only a vernacular name and did not provide a description. See Goncharova (1989: 118).

LUTRARIINAE Gray, 1853 [1 January]

Reference: *Annals and Magazine of Natural History*, ser. 2, 11(61): 42

Type genus: *Lutraria* Lamarck, 1799

Remarks: Original spelling Lutrariana. -idae, Pelseneer (1906: 273).

LYMNOCARDIINAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous fauna of southern India*, vol. 3, parts 1–4: 8b, 205, 211

Type genus: †*Lymnocardium* Stoliczka, 1870

Remarks: -idae, Keen (in Moore, ed., 1969: 590); -ini, Kafanov & Popov (1977: 60).

LYONSIELLIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 533

Type genus: *Lyonsiella* G. O. Sars, 1872

Remarks: Declared again new by Scarlato & Starobogatov (in Nevesskaja et al., 1971: 19).

LYONSIIDAE P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (11): 1162

Type genus: *Lyonsia* Turton, 1822

LYRODESMATINAE P. Fischer, 1886 [30 April]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (10): 982

Type genus: †*Lyrodesma* Conrad, 1841

Remarks: -idae, Ulrich (1894: 486, 608); -oidea [as -acea], Cox (1960: 85).

LYRODONTIDAE Bronn, 1862

Reference: *Die Klassen und Ordnungen der Weichthiere (Malacozoa)*, 3(1): 474, 499

Type genus: †*Lyrodon* Goldfuss, 1837

Remarks: Original spelling Lyriodontidae, based on *Lyriodon* Dunker, 1851, an unjustified emendation of *Lyrodon*. -inae [as Lyriodontana], same reference.

MACCOYELLINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 165

Type genus: †*Maccoyella* Etheridge, 1892

MACOMINAE Olsson, 1961

Reference: *Mollusks of the tropical eastern Pacific, Panamic-Pacific Pelecypoda*: 377

Type genus: *Macoma* Leach, 1819

MACROCHLAMYDINAE Kasum-Zade, 2003

Reference: [Advance in research of Mesozoic bivalve mollusks in Azerbaijan Order Pectinoida: revision and systematics]: 47, 82

Type genus: †*Macrochlamys* Sacco, 1897

Remarks: Original spelling Macrochlamisinae, based on *Macrochlamis*, ruled by Opinion 2203 (2008) to be an incorrect original spelling of *Macrochlamys*. Invalid: type genus a junior homonym of *Macrochlamys* Gray, 1847 [Gastropoda].

MACRODONTPELLIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24

Type genus: †*Macrodontella* Assmann, 1916

MACRODONTINAE Meek & Hayden, 1865 [April]

Reference: *Smithsonian Contributions to Knowledge*, 14(172): 88

Type genus: †*Macrodon* Buckman, 1845

Remarks: -idae, Dall (1895a: 516). Invalid: Type genus a junior homonym of *Macrodon* Schinz, 1822 [Pisces]. See Parallelodontidae.

MACTRIDAE Lamarck, 1809

Reference: *Philosophie zoologique*: 318

Type genus: *Macra* Linnaeus, 1767

Remarks: Original spelling “Les Mactracées” (vernacular). First latinized, as Mactracea, by Children (1822: 86). -inae [as -ina], Gray (1853: 41); -oidea [as -acea], Dall (1895a: 556).

MACTROMYIDAE Cox, 1929 (1887)

Reference: *Proceedings of the Dorset Natural History and Archaeological Society*, 50: 179

Type genus: †*Mactromya* Agassiz, 1842

Remarks: Also spelled Mactromyacidæ by Cox (1935: 183). Cox treated *Unicardium* as a synonym of *Mactromya*, and introduced Mactromyidae as a replacement for Unicardiidae; Mactromyidae is in prevailing usage and it is maintained under Art. 40.2 with the priority of Unicardiidae (1887). -oidea, Scarlato & Starobogatov (1979a: 22).

MALIMANININAE Waterhouse, 2001 [1 July]

Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 112

Type genus: †*Malimanina* Waterhouse, 2001

MALLEIDAE Lamarck, 1818

Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 424

Type genus: *Malleus* Lamarck, 1799

Remarks: Original spelling “Les Malléacées” (vernacular). First latinized [as Malleacea] by Children (1823: 34). -inae [as “trib. Malleacea” below family Mytilidae], Mörch (1853: 49); -oidea, Nevesskaja et al. (1971: 15).

MALLETIINAE H. Adams & A. Adams, 1858 [January] (1846)

Reference: *The Genera of Recent Mollusca*, 2: 548

Type genus: *Malletia* Des Moulins, 1832

Remarks: When they established Malletiidae, H. & A. Adams did not cite Solenellidae, but placed *Solenella* G. B. Sowerby I, 1833, in the synonymy of *Malletia*. Malletiidae is in prevailing usage; it is conserved under Art. 40.2 with the priority of Solenellidae (1846). -idae, Eberzin (1960: 69); -oidea, Nevesskaja et al. (1971: 12).

MANTICULIDAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 18

Type genus: †*Mantacula* Waterhouse, 1960

MANZANELLIDAE Chronic, 1952 [February]

Reference: *Bulletin of the Geological Society of America*, 63(2): 139

Type genus: †*Manzanella* Girty, 1909

Remarks: -oidea, Nevesskaja et al. (1971: 12).

MARGARITANINAE Ortmann, 1910 [17 February]

Reference: *The Nautilus*, 23(9): 116

Type genus: *Margaritana* Schumacher, 1817

Remarks: -idae, Ortmann (1911b: 6). Invalid: placed on the Official Index by Opinion 495 (1957: 289). See Margaritiferinae.

MARGARITARIIDAE H. A. Vokes, 1964 [14 August]

Reference: *Tulane Studies in Geology*, 2(4): 136

Type genus: †*Margaritaria* Conrad, 1863

Remarks: No explicit description, but the family is declared monotypic and the type genus is described.

MARGARITIDAE Blainville, 1824

Reference: *Dictionnaire des Sciences Naturelles*, 32: 313

Type genus: *Margarita* Leach, 1814

Remarks: Original spelling Margaritacea. Also declared new [as Margaritadæ] by Swainson (1831: pl. 1).

MARGARITIFERIDAE Henderson, 1929 [July] (1910)

Reference: *The University of Colorado Studies*, 17(2): 53

Type genus: *Margaritifera* Schumacher, 1815

Remarks: When he established Margaritiferidae, Henderson commented that *Margaritifera* was replacing *Margaritana* and he thus was probably, although not explicitly, replacing Margaritanidae by Margaritiferidae. Margaritiferidae is in prevailing usage and is conserved under Art. 40.2 with the priority of Margaritanidae (1910). -inae, Henderson (1935: 68). Placed on the Official List by Opinion 495 (1957: 289), but attributed in error to Haas (1940).

MARIKELLIIDAE Iredale & McMichael, 1962 [30 May]

Reference: *The Australian Museum, Sydney, Memoir*, 11: 19

Type genus: *Marikellia* Cotton & Godfrey, 1938

Remarks: Not available: name only, no description.

MARTESIINAE Grant & Gale, 1931 [3 November]

Reference: *Memoirs of the San Diego Society of Natural History*, 1: 433

Type genus: *Martesia* G. B. Sowerby I, 1824

Remarks: Established as a substitute name for Jouannetiinae, based on *Jouannetia* Des Moulins, 1828, by Grant & Gale considered a synonym of *Martesia*. Both Martesiinae and Jouannetiinae are little used and there is no “prevailing usage” that would justify applying Art. 40.2. Priority should apply.

MARTINSONELLINAE Sha, 1993

Reference: [Sha Jin-geng] *Acta Palaeontologica Sinica*, 32(3): 290 [Chinese], 300 [English]

Type genus: †*Martinsonella* Hong [in Martinson], 1965

Remarks: Not available from Sha (1989, unpublished Ph.D. dissertation).

MATHERIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 21, 29

Type genus: †*Matheria* Billings, 1858

MCLEARNIINAE Shurygin & Lutikov, 1991

Reference: *Trudy Instituta Geologii i Geofiziki, Sibirskoe Otdelenie*, 769: 63

Type genus: †*Mclearnia* Crickmay, 1930

MCLELLANIINAE D. Wilson, 1983

Reference: *Smithsonian Contributions to Paleobiology*, 53: 486

Type genus: †*Mclellania* D. Wilson, 1983

Remarks: Described as a cirriped crustacean, but found to be based on a mineralogical aberration of *Mercenaria* (Carter et al., 1998: 999).

MECYNODONTIDAE Haffer, 1959 [May]

Reference: *Palaeontographica*, ser. A, 112(5–6): 176

Type genus: †*Mecynodon* Keferstein, 1857

MEDIONIDINAE Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 70, 287

Type genus: *Medionidus* Simpson, 1900

Remarks: -ini, same reference.

MEGADESMIDAE H. A. Vokes, 1967 [16 June]

Reference: *Bulletins of American Paleontology*, 51(232): 322

Type genus: †*Megadesmus* J. De C. Sowerby, 1839

Remarks: Introduced, in violation of Art. 40.1, as a replacement for Pachydomidae, based on *Pachydomus* J. Morris, 1845, an unnecessary nom. nov. pro *Megadesmus*. However the name Megadesmidae has been treated as valid by, e.g., Newell (in Moore, ed., 1969: 823). -inae, Waterhouse (2001: 144).

MEGALODIDAE Karczewski, 1992

Reference: *Prace Panstwonego Instytutu Geologicznego*, 140: 14, 29

Type genus: †*Megalodus* Goldfuss, 1837

Remarks: Original spelling Megalodusidae. -oidea [as -acea], same reference. *Megalodus* is originally an emendation of *Megalodon* J. De C. Sowerby, 1827, but it is treated by Karczewski as a valid genus; however, it is a junior homonym of *Megalodus* Rafinesque, 1815 [Hymenoptera], which renders Megalodidae invalid.

MEGALODONTIDAE J. Morris & Lycett, 1853

Reference: *A monograph of the Mollusca from the Great Oolite*. Part 2, Bivalves: 78

Type genus: †*Megalodon* J. De C. Sowerby, 1827

Remarks: Original spelling Megalonidae. Placed on the Official List by Opinion 1829 (1996: 66). -oidea [as -acea], Pompeckj (1912: 26).

MEGALONAIADINAE Heard & Guckert, 1970 [December]

Reference: *Malacologia*, 10(2): 338

Type genus: *Megalonaias* Utterback, 1915

Remarks: -ini, J. B. Burch (1975: 2).

MEGATRIGONIINAE van Hoepen, 1929

Reference: *Paleontologiese Navorsing van die Nasionale Museum*, 1(1): 3

Type genus: †*Megatrigonia* van Hoepen, 1929

Remarks: -oidea [as -acea] and -idae, M. R. Cooper (1991: 24, 25).

MELAXINAEINAE Habe, 1977

Reference: *Systematics of Mollusca in Japan (Bivalvia and Scaphopoda)*: 48

Type genus: *Melaxinaea* Iredale, 1930

Remarks: -idae [declared new], Scarlato & Starobogatov (1979a: 23, as Melaxineidae, based on *Melaxinea*, an incorrect subsequent spelling).

MELININAE Meek & Hayden, 1865 [April]

Reference: *Smithsonian Contributions to Knowledge*, 14(172): 28

Type genus: *Melina* Philipsson, 1788

Remarks: -idae, Ridewood (1903: 196). See also Isognomonidae.

MELLITERYCINAE Iredale & McMichael, 1962 [30 May]

Reference: *The Australian Museum, Sydney, Memoir*, 11: 20

Type genus: *Melliteryx* Iredale, 1924

Remarks: Not available: name only, no description. Ponder (1971: 138) suggested that Melliterycinae “may be a distinct group”, based on an anatomical character, but he did not explicitly treat it as a valid name. Not made available by Habe (1977: 141, as -idae, nomen nudum); nor from Higo & Goto (1993: 603, nomen nudum); nor from Lee (2002: 38, nomen nudum).

MERETRICINAE Gray, 1847 [November] (1838)

Reference: *Proceedings of the Zoological Society of London*, 15: 183

Type genus: *Meretrix* Lamarck, 1799

Remarks: Original spelling Meretricina. -idae [declared new], Frizzell (1936a: 415). When he established Meretricinae, Gray cited *Cytherea* Lamarck, 1805, in the synonymy of *Meretrix*, and Meretricinae can be considered a substitute name for Cythereinae. Meretricinae is conserved under Art. 40.2, with the priority of Cythereinae (1838).

MERKLINICARDIINI Popov, 2001

Reference: [in Nevesskaja, Paramonova & Popov] *Paleontological Journal*, 35, supplementary issue 3: 149, 176

Type genus: †*Merklinicardium* Popov, 1982

Remarks: -ina, Bieler, Carter & Coan, herein.

MEROINAE Tryon, 1884

Reference: *Structural and systematic conchology*, 3: 179

Type genus: *Meroe* Schumacher, 1817

Remarks: Original spelling Meroëinae.

MESODESMATIDAE Gray, 1840 [16 October]

Reference: *Synopsis of the contents of the British Museum*, ed. 42: 134, 149

Type genus: *Mesodesma* Deshayes, 1832

Remarks: Original spelling Mesodesmidae. -inae, Dall (1895a: 557); -oidea [as -acea], Yonge & Allen (1986: 346). See also Paphiidae Gray, 1847.

MESOPEPLINI Waller, 2006

Reference: [in Shumway & Parsons, eds] *Scallops: Biology, ecology and aquaculture*: 8, 14

Type genus: *Mesopeplum* Iredale, 1929

MICRODONTPELLIDAE Gusev, 1969

Reference: *Soveshchanie po probleme "Puti i zakonomernosti istoricheskogo razvitiia zhivotnykh i rastitelnykh organizmov"*: 37

Type genus: †*Microdontella* Lebedev, 1944

Remarks: Attributed by Gusev to Lebedev (1944: 81), but Lebedev merely pointed out that *Microdontella* should be classified in a family of its own without formally naming it. Not available (no description) from Lebedev & Papin (1968: 134). Invalid: type genus a junior homonym of *Microdontella* Strand, 1934. See Senderzoniellinae.

MICRODONTIDAE Weir, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 407

Type genus: †*Microdonta* Khalfin, 1950

Remarks: Invalid: type genus a junior homonym of *Microdonta* Dejean, 1835, and *Microdonta* Hope, 1837.

MICROPOLIIDAE Iredale & McMichael, 1962 [30 May]

Reference: *The Australian Museum, Sydney, Memoir*, 11: 21

Type genus: *Micropolia* Laseron, 1953

Remarks: Not available: name only, no description.

MICROPTERIINAE Maillieux, 1931 [31 December]

Reference: *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 51: 64, 65

Type genus: †*Micropteria* Frech, 1891

Remarks: Independently declared new by Maillieux (1937: 67).

MILTHINAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 501

Type genus: *Miltha* H. Adams & A. Adams, 1857

MIMACHLAMYDINI Waller, 1993 [November]

Reference: *American Malacological Bulletin*, 10(2): 228

Type genus: *Mimachlamys* Iredale, 1929

MINETRIGONIINAE Kobayashi, 1954

Reference: *Japanese Journal of Geology and Geography, Transactions*, 25(1–2): 63

Type genus: †*Minetrigonia* Kobayashi & Katayama, 1938

Remarks: -idae, Fleming (1987: 24).

MIODOMERIDINAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 553

Type genus: †*Miodomeris* Chavan, 1938

Remarks: -idae, Scarlato & Starobogatov (1979a: 23, 35).

MODELLNAIINAE Brandt, 1974

Reference: *Archiv für Molluskenkunde*, 105(1–4): 301

Type genus: *Modellnaia* Brandt, 1974

MODIOLARCIDAE Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 412

Type genus: *Modiolarca* Gray, 1842

Remarks: Original spelling Modiolarcadae. -inae, P. Fischer (1886: 965). When he established the family, Gray used *Modiolarca* in

the sense he had used it in 1847 for *Modiola trapezina* Lamarck, 1819 [i.e., in the sense of *Gaimardia*], and not in the sense he had earlier (1842, 1843) used *Modiolarca* for *Mytilus impactus* Hermann, 1782 [i.e., for a species of Mytilidae: Musculinae]. The name Modiolarcidae was thus based on a misidentified type genus and, under Art. 65.2.1, the Case should be brought to the Commission. See also Gaimardiidae.

MODIOLIDAE G. Termier & H. Termier, 1950

Reference: *Paléontologie marocaine*. 2, *Invertébrés de l'ère primaire*. Fascicule 3, *Mollusques*: 81, 85

Type genus: *Modiolus* Lamarck, 1799

Remarks: -ini, Keen (1958: 54); -inae, Bowden & Heppell (1966: 104). Under Art. 23.9 of the Code, Jolyidae Bourguignat, 1877, is here declared a *nomen oblitum* and Modiolidae G. Termier & H. Termier, 1950, a *nomen protectum*, based on usage in at least the following publications: Abbott (1974: 434), Bernard (1983: 19), Bernard et al. (1993: 31), Beu & Maxwell (1990: 255, 309, 338, 395), Bieler & Mikkelsen (2006: 229), Boss (1982: 1109), Bowden & Heppell (1966: 104), Coan & Scott (1997: 6), Coan et al. (2000: 181), Habe (1977: 53; 1981: 45), Higo & Goto (1973: 559), Keen (1958: 54), Kilias (1997: 191), Morton et al. (in Beesley et al., eds., 1998: 250), Naumov et al. (1987: 224), Nord-sieck (1969: 31), Oliver (1992: 52), Sabelli et al. (1990: 81, 284), Scarlato (1981: 223), Scarlato & Starobogatov (1979b: 24), Soot-Ryen (in Moore, ed., 1969: 278), Steiner & Hammer (2000: 14, 26), Vaught (1989: 116), Wang (1997: v, 163, 242). To our knowledge, the name Jolyidae has not been used as valid after 1899.

MODIOLODONTIDAE Fang & N. J. Morris, 1997

Reference: *Palaeoworld*, 7: 62

Type genus: †*Modiolodon* Ulrich, 1894

MODIOLOPSIDAE P. Fischer, 1886 [30 April]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (10): 989

Type genus: †*Modiolopsis* Hall, 1847

Remarks: Independently declared new by Ulrich (1894: 485, 500). -inae, Liljedahl (1994: 82); -oidea [as -acea], Fang & Morris (1997: 62).

MODIOMORPHIDAE S. A. Miller, 1877

Reference: *The American Palaeozoic fossils*: 180

Type genus: †*Modiomorpha* Hall, 1869

Remarks: -oidea [as -acea], Newell (1965: 18); -inae, Babin (1977: 66). Precedence over simultaneously published Palanatinidae determined by First Reviser action by Carter, herein.

MONOCONDYLAEINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 175

Type genus: *Monocondylaea* d'Orbigny, 1835

Remarks: -idae, Morretes (1949: 24); -ini, Bonetto (1966: 5).

MONOPLEURIDAE Munier-Chalmas, 1873 [31 January]

Reference: *Journal de Conchyliologie*, 21(1): 73

Type genus: †*Monopleura* Matheron, 1842

Remarks: -inae, MacGillavry (1937: 37); -oidea, Yanin (1990: 65).

MONOPTERIIDAE Newell, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 297

Type genus: †*Monopteria* Meek & Worthen, 1866

MONOTINAE P. Fischer, 1886 [30 April]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (10): 951

Type genus: †*Monotis* Bronn, 1830

Remarks: Original spelling Monotiinae. -idae, Kittl (1912: 166); -oidea, Begg & Campbell (1986: 727).

MONTACUTIDAE W. Clark, 1855

Reference: *A history of the British marine testaceous Mollusca*: 94

Type genus: *Montacuta* Turton, 1822

Remarks: -inae, Abbott (1974: 471).

MONTANARIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 22, 33

Type genus: †*Montanaria* Spriesterbach, 1909

MONTICULINIDAE A. Ivanov, 1995

Reference: *Paleontologicheskii Zhurnal*, 1995(3): 33

Type genus: †*Monticulina* A. Ivanov, 1995

Remarks: -inae, same reference.

MULLERIIDAE Deshayes, 1832 [29 September]

Reference: *Encyclopédie méthodique, Histoire naturelle des vers*, 2: table facing page 553

Type genus: *Mulleria* Férussac, 1823

Remarks: Original spelling (family) "Mullerie" (vernacular). First latinized [as Mülleriae] by Herrmannsen (1847: 61), who attributed the

name to Deshayes. Priority over simultaneously published Etheriidae determined by First Reviser action by Gill (1871: 20). -inae [as Mülleriana], Bronn (1862: 474, 499); -oidea [as Muelleracea], Gill (1871: 20).

MUSCULIDAE Iredale, 1939 [25 February]
Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 230
Type genus: *Musculus* Röding, 1798
Remarks: Name only, no description. Diagnosed [as -inae] by Kuroda, Habe & Oyama (1971: 550 [Japanese text], 359 [English text]).

MUSCULINAE Starobogatov, 1984
Reference: [in Stadnichenko] *Fauna Ukraini*, 29(9): 155
Type genus: *Musculium* Link, 1807

MUTELIDAE Gray, 1847 [November]
Reference: *Proceedings of the Zoological Society of London*, 15: 197
Type genus: *Mutela* Scopoli, 1777
Remarks: Original spelling Muteladae. -inae, Kobelt (1881: 360); -oidea [as -acea], Parodiz & Bonetto (1963: 186).

MWERUELLINAE Pain & F. R. Woodward, 1968 [29 March]
Reference: *Revue de Zoologie et Botanique Africaines*, 77(1–2): 200
Type genus: *Mweruella* Haas, 1936

MYADESMATIDAE B. L. Clark, 1922 [7 September]
Reference: *University of California Publications, Bulletin of the Department of Geological Sciences*, 14(4): 115
Type genus: †*Myadesma* B. L. Clark, 1922
Remarks: Original spelling Myadesmidae.

MYALININAE Frech, 1891
Reference: *Abhandlungen zur Geologischen Specialkarte von Preussen und den Thüringischen Staaten*, 9(3): 397 [137]
Type genus: †*Myalina* de Koninck, 1842
Remarks: -idae, Dall (1896: 372).

MYCETOPODIDAE Gray, 1840 [16 October]
Reference: *Synopsis of the contents of the British Museum*, ed. 42: 138, 150
Type genus: *Mycetopoda* d'Orbigny, 1835
Remarks: -inae [as Mycetopedina], Gray (1854a: 416); and also Mycetopinae (based on *Mycetopus* d'Orbigny, 1840, an unjustified emendation of *Mycetopoda*), H. Adams & A. Adams (1857: 504).

MYIDAE Lamarck, 1809
Reference: *Philosophie zoologique*: 319
Type genus: *Mya* Linnaeus, 1758
Remarks: Original spelling “Les myaires” (vernacular). First latinized [as Myacea] by Goldfuss (1820: 613). Spelling Myacidae (first used by d'Orbigny 1846 [in 1835–1846]: 501) also used by 19th century authors. -oidea [as -acea], Gill (1871: 18); -inae [as -ana], Bronn (1862: 476, 502).

MYLLITIDAE Iredale & McMichael, 1962 [30 May]
Reference: *The Australian Museum, Sydney, Memoir*, 11: 20
Type genus: *Myllita* d'Orbigny & Récluz, 1850
Remarks: Not available: name only, no description. Not made available by Ponder (1971: 138, 139, as -inae; no description), nor by Powell (1979: 392, as -inae; no description).

MYOCHAMIDAE P. P. Carpenter, 1861
Reference: *Annual Report of the Board of Regents of the Smithsonian Institution* for 1860: 251
Type genus: *Myochama* Stutchbury, 1830
Remarks: -inae [as -ana], Bronn (1862: 476); -oidea, Scarlato & Starobogatov (1979a: 22, 32).

MYOCONCHIDAE Newell, 1957 [29 November]
Reference: *American Museum Novitates*, 1857: 6
Type genus: †*Myoconcha* J. De C. Sowerby, 1824
Remarks: -inae, Chavan (in Moore, ed., 1969: 547).

MYODAKRYOTIDAE Tunnicliff, 1987 [4 December]
Reference: *Palaeontology*, 30(4): 684
Type genus: †*Myodakryotus* Tunnicliff, 1987
Remarks: -oidea, Nevesskaja (2003: 616).

MYONERIDAE Scarlato & Starobogatov, 1983
Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 13
Type genus: *Myonera* Dall & E. A. Smith, 1886

MYONIIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*, 80: 22, 32
Type genus: †*Myonia* Dana, 1847
Remarks: Not available (established conditionally) from Myoniini [as -ides] Waterhouse (1969: 21, 28). -inae, Waterhouse (1987: 170).

MYOPHOLADIDAE Cox, 1964 [April]

Reference: *Proceedings of the Malacological Society of London*, 36(1): 43

Type genus: †*Myopholas* Douvillé, 1907

MYOPHORELLINAE Kobayashi, 1954

Reference: *Japanese Journal of Geology and Geography, Transactions*, 25(1–2): 68

Type genus: †*Myophorella* Bayle, 1878

Remarks: -idae and -oidea [as -acea], M. R. Cooper (1991: 9).

MYOPHORICARDIIDAE Cox & Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 580

Type genus: †*Myophoricardium* Wöhrmann, 1889

Remarks: Not available (no description) from Chavan (in H. A. Vokes, 1967: 259). See also Myophoriopidae.

MYOPHORIIDAE Bronn, 1849

Reference: *Index Palaeontologicus*, Abt. 2, B: 289

Type genus: †*Myophoria* Bronn, 1834

Remarks: Original spelling Myophorieae. -oidea [as -acea], M. R. Cooper (1991: 4).

MYOPHORIOPIDAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 565

Type genus: †*Myophoriopis* Wöhrmann, 1889

Remarks: Not available (no description), and apparently intended to refer to Myophoricardiidae.

MYRAKEENINI Harry, 1985 [1 October]

Reference: *The Veliger*, 28(2): 138

Type genus: *Myrakeena* Harry, 1985

MYRTEINAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 499

Type genus: *Myrtea* Turton, 1822

MYSELLINAE F. R. Bernard, 1983 [about 15 April]

Reference: *Canadian Special Publication of Fisheries and Aquatic Sciences*, 61: 32, 68

Type genus: *Mysella* Angas, 1877

Remarks: Not available (name only, no description) from Iredale & McMichael (1962: 20).

MYSIDIELLIDAE Cox, 1964 [April]

Reference: *Proceedings of the Malacological Society of London*, 36(1): 44

Type genus: †*Mysidiella* Cox, 1964

Remarks: -oidea, Scarlato & Starobogatov (1979a: 20, 29).

MYSIDIOPTERINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 131

Type genus: †*Mysidioptera* Salomon, 1895

Remarks: Original spelling Mysidiopterinae, based on *Mysidoptera*, an incorrect subsequent spelling of the type genus.

MYSIIDAE Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 410

Type genus: *Mysia* Lamarck, 1818

Remarks: Original spelling Mysiadae. When he established the family Mysiidae, Gray used *Mysia* in the sense of Brown (1827), i.e. for a species of Ungulinidae. However, Leach's MS name *Mysia* was first made available by Lamarck for *Venus undata* Pennant, a species now placed in the Veneridae. Under Art. 41, the case should be brought to the Commission. As Mysiidae would have priority over Ungulinidae Gray, 1854 [1 July], stability is best served by treating Mysiidae in the synonymy of Veneridae.

MYTILINAE Rafinesque, 1815

Reference: *Analyse de la nature*: 147

Type genus: *Mytilus* Linnaeus, 1758

Remarks: Original spelling (subfamily) Mytilidia. Blainville (1814: 179) had earlier used the vernacular “les mytilacées”, but the name Mytilidae is not generally considered to date from that author. -idae [as Mytilacea], Goldfuss (1820: 610); -oidea [as -acea], Tryon (1884: 261); -ini, Kafanov (1984: 45).

MYTILOIDINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 13

Type genus: †*Mytiloides* Brongniart, 1822

Remarks: Name only, no description. Available through its use as a valid name, e.g. by Aliev (1958: 134, as Mytiloinae [declared new, but not diagnosed]).

NAIADA Lamarck, 1818

Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 423

Remarks: Original spelling “Nayades” (vernacular). Latinized [as Naiada] by Children (1823: 23), and [as Naiidae] by Broderip (1839: 319); -oidea [as Naiades], Gill (1871: 20). Not available: not based on a genus.

NAIADITIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*, 80: 20, 28

Type genus: †*Naiadites* Dawson, 1860

NAKAMURANAIADIDAE Guo, 1981
Reference: *12th Annual Conference of the Palaeontological Society of China. Selected Papers*: 61

Type genus: †*Nakamuranaia* Suzuki, 1943

NANNONAIINAE Modell, 1942 [15 October]
Reference: *Archiv für Molluskenkunde*, 74(5–6): 190

Type genus: *Nannonaia* Haas, 1913

Remarks: Precedence of Rectidentinae Modell, 1942, over simultaneously published Nannonaiinae determined by First Reviser action by Bieler et al., herein.

NANOGRINI Malchus, 1990
Reference: *Berliner Geowissenschaftliche Abhandlungen*, ser. A, 125: 109

Type genus: †*Nanogyra* Beurlen, 1958

NATALISSIMIDAE Waterhouse, 2008 [28 March]
Reference: *Earthwise*, 8: 50, 51

Type genus: †*Natalissima* Waterhouse, 2008

Remarks: -inae, Waterhouse, same reference.

NATASIINAE Sánchez, 1997 [June]
Reference: *Geobios, Mémoire spécial*, 20: 472
Type genus: †*Natasia* Sánchez, 1995

NAVICULIDAE MacNeil, 1937 [15 November]
Reference: *Journal of the Washington Academy of Sciences*, 27(11): 457

Type genus: *Navicula* Blainville, 1825

Remarks: Established as a substitute name for Arcidae when *Arca antiquata* was considered the type species of *Arca*. However, Opinion 189 (1945: 95, 105) ruled that *Arca noae* Linnaeus, 1758, is the type species of *Arca*.

NEAERIDAE Hidalgo, 1916
Reference: *Fauna malacologica de Espana, Portugal y las Baleares. Moluscos testaceos marinos*: 98

Type genus: *Neaera* Gray in Griffith & Pidgeon, 1833

Remarks: Invalid: type genus a junior homonym of *Neaera* Robineau-Desvoidy, 1830 [Diptera].

NEAEROPOROMYIDAE Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 12

Type genus: †*Neaeroporomya* Cossmann, 1886

Remarks: -oidea, same reference.

NEILONELLINAE Schileyko, 1989
Reference: *Trudy Instituta Okeanologii*, 123: 93

Type genus: *Neilonella* Dall, 1881

Remarks: Not available (no description) from Allen (1978: 390, as -idae). Established independently [as -idae n. fam.] by Fasulo (1990: 8) as a replacement name for Saturniidae Allen & Hannah, 1986, invalid because its type genus is a junior homonym; also -idae, Beu & Maxwell (1990: 393).

NEITHEINAE Sobetski, 1960
Reference: *Paleontologicheskii Zhurnal*, 1960(2): 68

Type genus: †*Neithea* Drouet, 1825

Remarks: -idae, Sobetski (1982: 114).

NEKLANIIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*, 80: 20, 28

Type genus: †*Neklania* Růžicka & Přibyl, 1953

Remarks: Original spelling Necklaniidae, based on *Necklania*, an incorrect subsequent spelling of the type genus.

NEMOCARDIINAE Savazzi, 1985
Reference: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 170(3): 316, 317

Type genus: †*Nemocardium* Meek, 1876

Remarks: Not available: name only, no description. Savazzi used the name Nemocardiinae without declaring it new, and apparently as a lapsus for Protocardiinae; see Schneider (1995: 341).

NEMODONTINAE Stephenson, 1941
Reference: *The University of Texas Publication*, 4101: 81

Type genus: †*Nemodon* Conrad, 1869

Remarks: Name only, no description. Available through its use as a valid name, e.g., by Scarlato & Starobogatov (1979b: 23, as -idae [declared new and diagnosed]).

NEOCOMICERAMINAE Tsagareli & Gambashidze, 1984

Reference: *Paleontologicheskii Sbornik [Lwow]*, 21: 52

Type genus: †*Neocomiceramus* Pochialainen, 1972

Remarks: Name only, no description. Not available under Art. 13.2.1, unless discovery of an author who used the name before 2000.

NEOLEPTONIDAE Thiele, 1934

Reference: *Handbuch der systematischen Weichtierkunde*, 2: 860

Type genus: *Neolepton* Monterosato, 1875

Remarks: -inae [declared new], F. Nordsieck (1969: 88).

NEOMIODONTIDAE Casey, 1955 [30 December]

Reference: *Proceedings of the Malacological Society of London*, 31(5–6): 209

Type genus: †*Neomiodon* P. Fischer, 1887

Remarks: -inae, Hayami (1965b: 131).

NEOPISIDIINAE Korniushev, 1989

Reference: *Zoologicheskii Zhurnal*, 68(11): 22

Type genus: *Neopisidium* Odhner, 1921

NEOPYCNODONTINI Harry, 1985 [1 October]

Reference: *The Veliger*, 28(2): 132

Type genus: *Neopycnodonte* Stenzel [in Moore], 1971

NEOTRIGONIINAE Kobayashi, 1954

Reference: *Japanese Journal of Geology and Geography, Transactions*, 25(1–2): 63

Type genus: *Neotrigonia* Cossmann, 1912

Remarks: Name only, no description. Available through its use as a valid name, e.g., by Eberzin (1960: 95).

NEUQUENITRIGONIINAE H. A. Leanza, 1993 [20 October]

Reference: *Bulletins of American Paleontology*, 105(343): 25

Type genus: †*Neuquenitrigonia* H. A. Leanza & Garate, 1987

NIPPONONAIIDAE Chen, 1988

Reference: [Chen Jinhua] *Advances in Science of China, Earth Sciences*, 2: 143, 144

Type genus: †*Nippononaia* Suzuki, 1941

Remarks: Not available (no description) from Kobayashi (1968: 130, as *Nippononaiadiidae*). -inae, same reference.

NODULARIINAE Starobogatov & Zatravkin, 1987

Reference: [in Zatravkin & Bogatov] *Krupnye dvustvorchatye molliuski presnykh i solonovatykh vod Dalnego Vostoka SSSR*: 25

Type genus: *Nodularia* Conrad, 1853

NOETIINAE Stewart, 1930 [9 August]

Reference: *The Academy of Natural Sciences of Philadelphia, Special Publication*, 3: 78

Type genus: *Noetia* H. Adams & A. Adams, 1857

Remarks: Original spelling Noetinae. -idae [as Noetidae], established independently by MacNeil (in Stephenson, 1937: 449, 457).

NORDENSKJOELDIIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25

Type genus: †*Nordenskjöldia* Wilckens, 1910

NOTOTRIGONIINAE Skwarko, 1963

Reference: *Commonwealth of Australia, Department of National Development, Bureau of Mineral Resources, Geology and Geophysics, Bulletin*, 67: 12, 22

Type genus: †*Nototrigonia* Cox, 1952

NOVACULININAE Ghosh, 1920 [3 June]

Reference: *Records of the Indian Museum*, 19(2): 64

Type genus: *Novaculina* Benson, 1830

Remarks: -idae, Habe (1977: 225, in the synonymy of Pharellidae).

NUCINELLIDAE H. A. Vokes, 1956a [20 July]

Reference: *Journal of Paleontology*, 30(3): 652

Type genus: †*Nucinella* S. V. Wood, 1850

Remarks: Name only, no description, but Vokes may have intended Nucinellidae as a replacement name for Nuculinidae because he listed *Nuculina* d'Orbigny, 1844, as a synonym of *Nucinella*. He may also have established Nucinellidae because he had found Nuculinidae to be invalid through homonymy of its type genus. It is thus unclear whether Nucinellidae takes the priority of Nuculinidae (1952) under Art. 40.2. -oidea [as -acea], Kuroda, Habe & Oyama (1971: 513 [Japanese text], 324 [English text]).

NUCULANIDAE H. Adams & A. Adams, 1858 [November] (1854)

Reference: *The Genera of Recent Mollusca*, 2: 660

Type genus: *Nuculana* Link, 1807

Remarks: Established as a substitute name for Ledidae, based on *Leda* Schumacher, 1817, by H. & A. Adams treated as a synonym of *Nuculana*. Nuculanidae is in prevailing use.

age, and is conserved under Art. 40.2 with the priority of *Ledidae* (1854). -inae, same reference, and also declared new by Glibert & van de Poel (1965: 18); -oidea [as superfamily *Nuculanicae*], Stenzel et al. (1957: 46), and also declared new by Sanders & Allen (1973: 239).

NUCLARCIDAE Pojeta & Stott, 2007 [October]
Reference: *Canadian Journal of Earth Sciences*, 44(10): 1482
Type genus: †*Nucularca* Pojeta & Stott, 2007

NUCULIDAE Gray, 1824
Reference: *A supplement to the appendix of Captain Parry's voyage for the discovery of a north west passage ...*, Appendix: ccxli
Type genus: *Nucula* Lamarck, 1799
Remarks: -inae [as -ina], Gray (1854a: 417); -oidea [as -acea], Dall (1896: 363).

NUCULINIDAE Chonic, 1952 [February]
Reference: *Bulletin of the Geological Society of America*, 63(2): 139
Type genus: †*Nuculina* d'Orbigny, 1844
Remarks: Invalid: Type genus a junior homonym of *Nuculina* Porro, 1837. See *Nucinellidae*.

NUCULITIDAE Bradshaw, 1999
Reference: *Association of Australasian Palaeontologists, Memoir*, 20: 56
Type genus: †*Nuculites* Conrad, 1841
Remarks: -inae, Babin, Jaouen & Racheboeuf (2001: 14).

NUCULOMINAE Maxwell, 1988 [December]
Reference: *Journal of Conchology*, 33(2): 87
Type genus: †*Nuculoma* Cossmann, 1907

NYASSIDAE S. A. Miller, 1877
Reference: *The American Palaeozoic fossils*: 180
Type genus: †*Nyassa* Hall, 1869
Remarks: -oidea, Nevesskaja et al. (1971: 13).

NYMPHACEA Lamarck, 1818
Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 423, 466, 508
Remarks: Original spelling "Les Nymphacées" (vernacular). First latinized [as *Nymphacea*] by Children (1823: 303) and later [as *Nymphidae*] by Broderip (1839: 319). Established as a family-group name and not available as such (not based on a genus).

OBLIQUIDONTINAE Astafieva-Urbajtis, 1994
Reference: *Paleontologicheskii Zhurnal*, 1994(2): 113
Type genus: †*Obliquidon* Astafieva-Urbajtis, 1994

OBSOLETIFORMINI Paramonova, 2001
Reference: [in Nevesskaja, Paramonova & Popov] *Paleontological Journal*, 35, supplementary issue 3: 149, 179
Type genus: †*Obsoletiformes* Kojumdieva, 1969
Remarks: -ina, Bieler, Carter & Coan, herein.

ODONTOGRYPHAEINI Vialov, 1983
Reference: *Doklady Akademii Nauk Ukrainskoi SSR*, ser. B, 11: 7
Type genus: †*Odontogryphaea* Ihering, 1903
Remarks: Not available: no description.

OLIGODONTELLINAE Starobogatov, 1987
Reference: [in Betekhtina, Starobogatov & Jatsuk] *Akademiia Nauk SSSR, Sibirskoe Otdelnie, Institut Geologii i Geofiziki, Trudy*, 688: 40
Type genus: †*Oligodontella* Gusev, 1963

ONCOPHORIDAE Davitashvili, 1934
Reference: *Biulleten' Moskovskogo Obshchestva Ispytatelei Prirody*, new ser., 42, *Otdel Geologicheskii*, 12(3): 396, 409
Type genus: †*Oncophora* Rzehak, 1882
Remarks: Invalid: Type genus a junior homonym of *Oncophora* Diesing, 1851 [Nematoda]. See *Rzehakiidae*.

OPINAE Chavan, 1952
Reference: *Cahiers Géologiques de Thoiry*, 15: 126
Type genus: †*Opis* Deshayes, 1835
Remarks: Original spelling *Opisinae*; spelling corrected to *Opinae* by Chavan (in Moore, ed., 1969: 571). -idae, Termier & Termier (in Termier et al., 1977: 85). Potentially homonym of *Opisidae* Lowry & Stoddart, 1995; based on *Opisa* Boeck, 1876 [Amphipoda].

OPOKIELLIDAE Kanev, 1983
Reference: *Akademiia Nauk SSSR, Komi Filial, Trudy Instituta Geologii*, 44: 23
Type genus: †*Opokiella* Plotnikov, 1949

ORBICULOPECTININAE Waterhouse, 2001 [1 July]
Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 116, 130

Type genus: †*Orbiculopecten* Gonzalez, 1978
 Remarks: Original spelling Orbiculipectininae.
 -ini, same reference.

ORETIINAE Waterhouse, 2008 [28 March]
 Reference: *Earthwise*, 8: 38
 Type genus: †*Oretia* Marwick, 1953
 Remarks: Original spelling Oretinae.

ORIOCRASSATELLINAE Boyd & Newell, 1968
 Reference: *American Museum Novitates*, 2328:
 23, 28
 Type genus: †*Oriocrassatella* Etheridge, 1907

OROBITELLINAE F. R. Bernard, 1983 [about 15
 April]
 Reference: *Canadian Special Publication of
 Fisheries and Aquatic Sciences*, 61: 32, 68
 Type genus: *Orobitella* Dall, 1900

ORTHOCARDIINAE Schneider, 2002 [November]
 Reference: *Zoological Journal of the Linnean
 Society*, 136(3): 367
 Type genus: †*Orthocardium* Tremlett, 1950

ORTHOCERAMINAE Heinz, 1932
 Reference: *Mitteilungen aus dem Mineralo-
 gisch-Geologischen Staatsinstitut in Ham-
 burg*, 13: 6
 Type genus: †*Orthoceramus* Heinz, 1932
 Remarks: Not available: no description, and
 type genus not an available name under Art.
 13.1.1 (no description). Used but not made
 available by Aliev (1958: 134).

ORTHONOTIDAE S. A. Miller, 1877
 Reference: *The American Palaeozoic fossils*:
 180
 Type genus: †*Orthonota* Conrad, 1841
 Remarks: -oidea, Scarlato & Starobogatov
 (1979a: 21, 31).

OSCILLOPHINI Malchus, 1990
 Reference: *Berliner Geowissenschaftliche
 Abhandlungen*, ser. A, 125: 102
 Type genus: †*Oscillopha* Malchus, 1990

OSCU LIGERIDAE Yanin, 1990
 Reference: [in Menner, ed.] *Sistematika i filo-
 geniia bespozvonochnykh. Kriterii vydeleniia
 vychikh taksonov*: 67
 Type genus: †*Osculigera* Kühn, 1932

OSTEODESMATIDAE Couthouy, 1839 [February]
 Reference: *Boston Journal of Natural History*,
 2(2): 129

Type genus: *Osteodesma* Blainville, 1827
 Remarks: Established as “Ostéodesmes” (ver-
 nacular) by Deshayes (1832: table facing p.
 553); first latinized as *Osteodesmacea* by
 Couthouy who attributed the name to De-
 shayes. See Thraciidae.

OSTREIDAE Rafinesque, 1815
 Reference: *Analyse de la nature*: 148
 Type genus: *Ostrea* Linnaeus, 1758
 Remarks: Original spelling Ostreacia. Placed on
 the Official List by Opinion 356 (1955: 105);
 Opinion 356 also treated Ostracea [Blainville,
 1825: 519] and Ostreadae [Fleming, 1828:
 392] as “junior synonyms”. The Opinion did
 not consider the vernacular “Les ostracées”,
 used by Lamarck (1809: 317, and subsequent
 works). -inae [as Ostreana], Bronn (1862:
 474, 498); -oidea [as -acea], Gill (1871: 22)
 [Stenzel (1971: 1097) attributed superfamily
 rank to Schweigger (1820: 712); Schweigger
 did use the spelling Ostreacea, but the con-
 text indicates that family rank was meant];
 -ini, Chiplonkar & Badve (1979: 443).

OTAPIRIINAE Waterhouse, 1982
 Reference: *New Zealand Geological Survey
 Paleontological Bulletin*, 49: 41
 Type genus: †*Otapiria* Marwick, 1935
 Remarks: -ini, Waterhouse (2001: 124); -idae,
 Waterhouse (2008: 166).

OZOMIIDAE Starobogatov, 1977
 Reference: *Biulleten' Moskovskogo Obshchest-
 va Ispitatelei Priroda, Otdel Geologicheskii*,
 52(4): 137
 Type genus: †*Ozomia* Walcott, 1924
 Remarks: Established as a family of bivalves,
 but now classified in the separate class
 Rostroconchia.

OXYGONA Latreille, 1824
 Reference: *Annales des Sciences Naturelles*,
 3: 332 and table
 Remarks: Original spelling “Oxygones”. Es-
 tablished as a family containing the genera
Mulleria, *Crenatula*, *Gervillia*, *Perna*, *Malleus*,
Pintadina, *Avicula*, and *Pinna*. Latinized
 by Berthold (1827: 202). Not available: not
 based on a genus.

OXYNAIINI Starobogatov, 1970
 Reference: *Fauna molliuskov i zooge-
 ograficheskoe raionirovanie kontinental'nykh
 vodoemov zemnogo shara*: 65, 284
 Type genus: *Oxynaia* Haas, 1913

OXYTOMINAE Ichikawa, 1958 [October]

Reference: *Palaeontographica*, ser. A, 111(5–6): 158

Type genus: †*Oxytoma* Meek, 1864

Remarks: -idae, Cox (1962: 592); -oidea, Waterhouse (2008: 163).

PACHYCARDIIDAE Cox, 1961 [December]

Reference: *Proceedings of the Malacological Society of London*, 34(6): 331

Type genus: †*Pachycardia* Hauer, 1857

Remarks: -inae, M. R. Cooper (1991: 4).

PACHYDACNINAE Andreescu, 1975

Reference: *6th Congress [Bratislava], Regional Committee on Mediterranean Neogene Stratigraphy*, volume 1: 145

Type genus: †*Pachydacna* Eberzin, 1955

Remarks: -ini, Taktakishvili (1987: 149); -ina, Bieler, Carter & Coan, herein.

PACHYDOMIDAE P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (11): 1077

Type genus: †*Pachydomus* J. Morris, 1845

Remarks: See Megadesmidae.

PACHYDONTINAE H. A. Vokes, 1945 [10 October]

Reference: *Bulletin of the American Museum of Natural History*, 86: 6, 21

Type genus: †*Pachydon* Gabb, 1869

PACHYRISMATIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 22, 32

Type genus: †*Pachyrisma* J. Morris & Lycett, 1850

PALAEANODONTINAE Modell, 1964 [20 July]

Reference: *Archiv für Molluskenkunde*, 93: 79

Type genus: †*Palaeanodonta* Amalitsky, 1895

Remarks: No description, but monotypic based on *Palaeanodonta*, which is diagnosed. -oidea / -idae, Starobogatov (1970: 58).

PALAEOCARDIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 20, 28

Type genus: †*Palaeocardia* Hall, 1865

PALAEOCARDITINAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 554

Type genus: †*Palaeocardita* Conrad, 1867

Remarks: -idae, Carter, herein.

PALAEOCONCHIDAE S. A. Miller, 1889 [after October]

Reference: *North American geology and palaeontology*: 458

Type genus: †*Palaeoconcha* S. A. Miller, 1889

PALAEOENTOLIINAE Romanov, 1985

Reference: *Iurskie pectinoidy Iuga SSSR*: 34

Type genus: †*Palaeoentolium* Romanov, 1985

Remarks: Not available (no description and type genus a nom. nud.) from Romanov (1984: 84).

PALAEOLOPHIDAE Malchus, 1990

Reference: *Berliner Geowissenschaftliche Abhandlungen*, ser. A, 125: 101, 102

Type genus: †*Palaeolopha* Malchus, 1990

Remarks: -inae / -ini, same reference.

PALAEOMUTELIDAE Lahusen, 1897

Reference: *Kratkii kurs paleontologii. Paleozoologia*: 355

Type genus: †*Palaeomutela* Amalitsky, 1891

Remarks: Independently declared new by Weir (in H. A. Vokes, 1967: 201, not available; in Moore, ed., 1969: 409) and Gusev (1969: 37).

PALAEONEILINAE Babin, 1966

Reference: *Mollusques bivalves et céphalopodes du Paléozoïque armoricain*: 71

Type genus: †*Palaeoneilo* Hall, 1869

Remarks: -idae, Babin & Jaouen (in Babin et al., 2001: 14). The spelling of the type genus has been fixed by Opinion 215 (1854).

PALAEONUCULINAE Carter, 2001

Reference: *American Malacological Bulletin*, 16(1–2): 225

Type genus: †*Palaeonucula* Quenstedt, 1930

PALAEOPHARIDAE Marwick, 1953

Reference: *New Zealand Geological Survey, Paleontological Bulletin*, 21: 69

Type genus: †*Palaeopharus* Kittl, 1907

PALAEOUNIONIDAE Amalitsky, 1892 [November]

Reference: *Palaeontographica*, 39(4–6): 201

Remarks: Not available: not based on a genus.

PALANATINIDAE S. A. Miller, 1877

Reference: *The American Palaeozoic fossils*: 180

Type genus: †*Palanatina* Hall, 1870

Remarks: Palaeoanatinidae [S. A. Miller, same reference: 199] is an unjustified emendation. Precedence of simultaneously published Modiomorphidae determined by First Reviser action by Carter, herein.

PALLIOLINAE Korobkov, 1960

Reference: [in Eberzin] *Osnovy Paleontologii. Molliuski. Pantzirnye, Dvustvorchatye, Lopatonogie*: 84

Type genus: *Palliolum* Monterosato, 1884

Remarks: Original spelling Pallioluminae. -ini, Waller (1993: 198).

PANDORINAE Rafinesque, 1815

Reference: *Analyse de la nature*: 146

Type genus: *Pandora* Bruguière, 1797

Remarks: Original spelling Pandoracia. -idae, Gray (1840b: 136, 150); -oidea [as -acea], Allan (1950: 300).

PANOPEINAE Bronn, 1862

Reference: *Die Klassen und Ordnungen der Weichthiere (Malacozoa)*, 3(1): 476, 502

Type genus: *Panopea* Ménard de la Groye, 1807

Remarks: Original spelling Panopaeana. Type genus placed on the Official List, with spelling *Panopea*, by Opinion 1414. -idae [as Panopidae], Récluz (1869: unnumbered table); -oidea [as -acea], Cossmann & Peyrot (1909: 192). Senior homonym of Panopeidae Ortmann, 1893 [Crustacea Xanthoidea].

PANTICAPAEINI Taktakishvili, 1987

Reference: *Sistematika i filogeniia plitsenykh cardiid Paratetisa*: 12, 188

Type genus: †*Panticapaea* Andrusov, 1923

Remarks: By First Reviser action, Nevesskaja et al. (2001: S191) determined that the simultaneously published Pontalmyrini has precedence over Panticapaeini. -ina, Bieler, Carter & Coan, herein.

PAPHIIDAE Gray, 1847 [November]

Reference: *Proceedings of the Zoological Society of London*, 15: 186

Type genus: *Paphia* Lamarck, 1799

Remarks: Original spelling Paphiadae. When he established Paphiidae, Gray included *Mesodesma* in the family, and he probably intended to introduce Paphiidae as a substitute name for Mesodesmatidae Gray, 1840. However, *Paphia* Lamarck, 1799, is a junior homonym of *Paphia* Röding, 1798 [Veneridae], which renders Paphiidae Gray, 1847, invalid. -inae, H. Adams & A. Adams (1857: 412).

PAPHIINAE Finlay, 1928 [10 August]

Reference: *Transactions of the New Zealand Institute*, 59: 278

Type genus: *Paphia* Röding, 1798

Remarks: Finlay established Paphiinae as a substitute name for Tapetinae, because *Paphia* Röding, 1798, is older than *Tapes* Megerle von Mühlfeldt. However, he did not treat the two genera as synonyms, and Art. 40.2 does not apply. Furthermore, Paphiinae Finlay, 1928, is a junior homonym of Paphiidae Gray, 1847, based on *Paphia* Lamarck, 1799 [Mesodesmatidae]. -idae [declared new], F. Nordsieck (1969: 115).

PARACYCLIDAE Johnston, 1993

Reference: *Memoir of the Association of Australasian Palaeontologists*, 14: 112

Type genus: †*Paracyclas* Hall, 1843

Remarks: Not available (no description) from H. A. Vokes (1967: 240, as Paracyclasinae).

PARADACNINAE Eberzin, 1967 [after 4 August]

Reference: *Trudy Paleontologicheskogo Instituta*, 112: 10

Type genus: †*Paradacna* Andrusov, 1909

Remarks: Not available (no description) from Eberzin (1965: 11). Eberzin attributed the name to himself with the date 1964, probably referring to the Proceedings of the first meeting of Soviet malacology [*Vsesoiuznoe soveshchanie po izucheniiu molliuskov*], which had taken place in 1961. The foreword to the Proceedings of the 2nd meeting says that the typescript Proceedings of the first meeting had a very restricted circulation. They were not available in the library of the Zoological Institute in Leningrad in 1990 and were thus unpublished in the sense of Code Chapter 3. -ini, Kafanov & Popov (1977: 60).

PARALLELODONTIDAE Dall, 1898 [October]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(4): 603, 604

Type genus: †*Parallelodon* Meek & Worthen, 1866

Remarks: Nom. nov. pro Macrodonatidae, invalid because its type genus is a junior homonym. -oidea [as -acea], MacNeil (1937: 457); -inae, Newell (in Moore, ed., 1969: 256).

PARARCIDAE Ulrich, 1894 [16 June]

Reference: *The Geological and Natural History Survey of Minnesota*, vol. 3(2), *Palaeontology*: 486

Type genus: †*Pararca* Hall, 1885

PARAVICULIDAE Gugenberger, 1935

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Akademie der Wissenschaften in Wien*, 144(1): 241

Remarks: Not available: not based on a genus name.

PARAYOLDIELLINAE Filatova & Schileyko, 1984

Reference: *Trudy Okeanologii Instituta*, 119: 133

Type genus: *Parayoldiella* Filatova, 1971

PARILIMYIDAE B. Morton, 1981 [8 December]

Reference: *Malacologia*, 21(1–2): 45

Type genus: *Parilimya* Melvill & Standen, 1899

Remarks: Independently declared new by Morton (1982). -oidea, Scarlato & Starobogatov (1983: 9).

PARREYSIINAE Henderson, 1935

Reference: *Geological Society of America, Special Papers*, 3: 69

Type genus: *Parreysia* Conrad, 1853

Remarks: Name only, no description. First diagnosed, and declared new, by Modell (1942: 186). -ini [and attributed to Henderson], Starobogatov (1970: 63).

PARVICARDIINI Kafanov & Starobogatov, 1977

Reference: [in Kafanov & Popov] *Paleontologicheskii Zhurnal*, 1977(3): 63

Type genus: *Parvicardium* Monterosato, 1884

PATINOPECTININAE Habe, 1977

Reference: *Systematics of Mollusca in Japan. Bivalvia and Scaphopoda*: 91

Type genus: †*Patinopecten* Dall, 1898

Remarks: Name attributed by Habe to Masuda (1962), but we have not detected this name in any of Masuda's papers. In a paper entitled "The so-called *Patinopecten* of Japan" (1963: 145–153), Masuda did not use Patinopectininae. Not available from MacNeil (1967, name only, no description). Habe (1977) appears to be the first author to make the name available.

PECTININAE Rafinesque, 1815

Reference: *Analyse de la nature*: 148

Type genus: *Pecten* O. F. Müller, 1776

Remarks: Original spelling Pectenina. -idae [as Pectenidae], Fleming (1822: 504); -oidea [as -acea], Gill (1871: 21); -ini [as Pectenini], Vaught (1989: 119). Some authors have attributed authorship of the family Pectinidae to

Wilkes (1810: 32), who recognized a family "Pectinoidae". Wilkes used the classification of da Costa. This has been discussed by Bouchet & Rocroi (2005: 5), who concluded that da Costa's usage of family and genus names is inconsistent with the principles of Articles 4.1 and 11.7.1.2 of the Code. Wilkes' contribution must be excluded from zoological nomenclature on the same grounds. Furthermore, Wilkes' family "Pectinoidae" includes *Vulsella*, whereas the "Pectens or Scallops" constitute another family.

PECTUNCULIDAE Leach, 1847 [1 October]

Reference: [in Gray] *Annals and Magazine of Natural History*, 20(133): 273

Type genus: *Pectunculus* Lamarck, 1799

Remarks: -inae [as Pectunculina], Gray (1854a: 417). Invalid: type genus a junior homonym of *Pectunculus* Huddesford, 1770. See also Glycymerididae.

PEDALIONIDAE Stephenson, 1923

Reference: *North Carolina Geological & Economic Survey, V. The Cretaceous formations of North Carolina*, 1: 123

Type genus: *Pedalion* Dillwyn, 1817

Remarks: Spelled Pedaliidae by Crickmay (1930: 48).

PEDIFERIA Rafinesque, 1815

Reference: *Analyse de la nature*: 147

Remarks: Taxon containing the genera *Egeria*, *Unio*, *Anodonta*, and *Pectunculus*. Established as a family-group name and not available as such (not based on a genus).

PEDINAE Bronn, 1862

Reference: *Die Klassen und Ordnungen der Weichthiere (Malacozoa)*, 3(1): 474, 498

Type genus: *Pedum* Bruguière, 1792

Remarks: Original spelling (subfamily) Pedana. Again declared new [as Peduminae] by Habe (1977: 92).

PEDUMINAE. See Pedinae.

PEGMAVALVULINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 180

Type genus: †*Pegmavalvula* Newell & Boyd, 1970

PENICILLINAE Gray, 1858b [9 November]

Reference: *Proceedings of the Zoological Society of London*, 26: 312

Type genus: *Penicillus* Bruguière, 1789

Remarks: Original spelling Penicillina. -idae, declared “nom. nov. (pro Aspergillidae Gray, 1858, excl. *Clavagella* Lamarck, 1818)”, Scarlato & Starobogatov (in Nevesskaja et al., 1971: 16); -oidea, Scarlato & Starobogatov (1979a: 22).

PEREGRINOCONCHIDAE Gu, Chen & Lan, 1976

Reference: [in Ma et al.] *Mesozoic fossils from Yunnan, China*, fasc. 1: 246

Type genus: †*Peregrinoconcha* Chen & Lan, 1976

Remarks: Original spelling Peregrinoconchiidae. -inae, Guo (1981: 193).

PERGAMIDIIDAE Cox, 1964 [April]

Reference: *Proceedings of the Malacological Society of London*, 36(1): 44

Type genus: †*Pergamidia* Bittner, 1891

Remarks: Independently declared new by Cox (in Moore, ed., 1969: 313). -inae, implied by Waterhouse (2008: 37, 38) by his establishing the sister subfamily Oretiinae, but not specifically named.

PERIPLOMATIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 531

Type genus: *Periploma* Schumacher, 1817

Remarks: Original spelling Periplomidae. -inae, Korobkov (1954: 208).

PERLAPOROMYIDAE Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 11

Type genus: *Perlaporomya* Scarlato & Starobogatov, 1983

PERMANOMIIDAE Carter, 1990

Reference: *Skeletal biomineralization: Patterns, processes and evolutionary trends*, 1: 253

Type genus: †*Permanomia* Newell & Boyd, 1970

PERMOCERAMINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 32

Type genus: †*Permoceramus* Waterhouse, 1970

PERMOPHORIDAE van de Poel, 1959 [June]

Reference: *Institut Royal des Sciences Naturelles de Belgique, Bulletin*, 35(16): 14

Type genus: †*Permophorus* Chavan, 1954

Remarks: Nom. nov. pro Pleurophoridae, invalid because its type genus is a junior homonym; this is not a situation covered by Art. 40, and Permophoridae does not take the priority of Pleurophoridae. -inae, Chavan (in Moore, ed., 1969: 543).

PERNARIINAE Rafinesque, 1815

Reference: *Analyse de la nature*: 147

Type genus: *Pernaria* Rafinesque, 1815

Remarks: Original spelling Pernaridia. *Pernaria* Rafinesque, 1815, is a substitute name for *Perna* Bruguière, 1789, non Philipsson, 1788. See also Pernidae.

PERNIDAE J. Fleming, 1828 [March]

Reference: *A history of British animals*: 381, 390

Type genus: *Perna* Bruguière, 1789

Remarks: Original spelling Pernadae. -inae, Tryon (1884: 277). Invalid: type genus a junior homonym of *Perna* Philipsson, 1788. See also Pernariinae and Isognomonidae.

PERNINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24

Type genus: *Perna* Philipsson, 1788

Remarks: The name of the type genus was cited without author/date, but is inferred from the context to be *Perna* Philipsson, 1788. Junior homonym of Pernidae Fleming, 1828, based on *Perna* Bruguière, 1789.

PERNOPECTININAE Newell, 1938 [28 July]

Reference: *State Geological Survey of Kansas Publications*, 10(1): 43

Type genus: †*Pernopecten* Winchell, 1865

Remarks: Name only, no description. Available through its use as a valid name, e.g. by Nevesskaja et al. (1971: 15, as -idae [not diagnosed]); -oidea [not diagnosed], Scarlato & Starobogatov (1979a: 21).

PERRIERINIDAE Marwick, 1928 [28 February]

Reference: *Transactions of the New Zealand Institute*, 58: 444

Type genus: *Perrierina* F. Bernard, 1897

PETRICOLIDAE d'Orbigny, 1840 [March]

Reference: *Histoire naturelle des îles Canaries*, 2(2), *Zoologie*: 109

Type genus: *Petricola* Lamarck, 1801

Remarks: First established as “Pétricolées” (vernacular) by Deshayes (1832: 552, 553)

and Deshayes (1839: table between pp. 212, 213). Coan (1997: 299) noted that the name Petricolidae had not been accepted by most later authors from these vernacular appearances, although both H. A. Vokes (1980) and Keen [in Moore, ed., 1969] attributed Petricolidae to Deshayes, 1839. -inae [as -ana], Bronn (1862: 476, 501).

PHARELLINAE Stoliczka, 1870 [1 September]
Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b, 96
Type genus: *Pharella* Gray, 1854
Remarks: -idae, Habe (1977: 225).

PHARINAE H. Adams & A. Adams, 1856 [June]
Reference: *The Genera of Recent Mollusca*: 342
Type genus: *Pharus* Gray, 1840
Remarks: -idae, Cosel (1990: 284).

PHASEOLIDAE Scarlato & Starobogatov, 1971
Reference: [in Nevesskaja et al.] *Paleontologicheskii Zhurnal*, 1971(2): 12
Type genus: *Phaseolus* Monterosato, 1875
Remarks: -oidea, same reference. See also under Radiidentidae.

PHESTIINAE Logan, 1967 [November]
Reference: *Palaeontological Society Monographs*, 121: 43
Type genus: †*Phestia* Chernyshev, 1951
Remarks: Established, in violation of Art. 40.1, as a substitute name for Polidevciinae, based on *Polidevcia* Chernyshev, 1951.

PHILOBRYINAE F. Bernard, 1897 [17 September]
Reference: *Journal de Conchyliologie*, 45(1): 8
Type genus: *Philobrya* J. G. Cooper, 1867
Remarks: -idae, Suter (1913: 856); -oidea, Coan, Scott & Bernard (2000: 150).

PHOLADELLIDAE S. A. Miller, 1877
Reference: *The American Palaeozoic fossils*: 180
Type genus: †*Pholadella* Hall, 1869
Remarks: -inae, P. Fischer (1887: 1176).

PHOLADIDAE Lamarck, 1809
Reference: *Philosophie zoologique*: 319
Type genus: *Pholas* Linnaeus, 1758
Remarks: Original spelling “Les pholadaires” (vernacular). First latinized by Children (1823:

82), in an English translation of Lamarck’s classification. -inae, Gray (1847: 187); -oidea, Gill (1871: 18).

PHOLADIDEINAE Taki & Habe, 1955
Reference: [in Kuroda, ed.] *Illustrated catalogue of Japanese shells*, 2(2): 9
Type genus: *Pholadidea* Turton, 1819
Remarks: Name only, no description. Not available under Art. 13.2.1, unless discovery of an author who used the name before 2000.

PHOLADOMYIDAE King, 1844 [1 November]
Reference: *Annals and Magazine of Natural History*, 14(92): 313
Type genus: *Pholadomya* G. B. Sowerby I, 1823
Remarks: -oidea [as -acea], Newell (1965: 21); -inae, Runnegar (1967: 62).

PHOLEOBIIDAE Leach, 1852
Reference: *A synopsis of the Mollusca of Great Britain*: 248, 255
Type genus: *Pholeobia* Blainville, 1819
Remarks: Original spelling Pholeobiadae.

PHYLLOCARDIINI Nevesskaja, 1986
Reference: [in Nevesskaja et al.] *Trudy Paleontologicheskogo Instituta*, 220: 189
Type genus: *Phyllocardium* P. Fischer, 1887
Remarks: -ina, Bieler, Carter & Coan, herein.

PHYSUNIONINI Starobogatov, 1970
Reference: *Fauna molljuskov i zoogeograficheskoe rajonirovanie kontinentalnykh vodoemov zemnogo shara*: 287
Type genus: *Physunio* Simpson, 1900

PICHLERIIDAE Scarlato & Starobogatov, 1979
Reference: *Trudy Zoologicheskogo Instituta*, 80: 21, 30
Type genus: †*Pichleria* Bittner, 1894
Remarks: Established the same year as new by Scarlato & Starobogatov (1979b: 23).

PILAEINI. See Pileini.

PILEINI Starobogatov, 1970
Reference: *Fauna molljuskov i zoogeografiskoe rajonirovanie kontinental’nykh vodoemov zemnogo shara*: 70, 287
Type genus: *Pilea* Simpson, 1900
Remarks: Original spelling Pilaeini, based on *Pilaea*, an incorrect subsequent spelling.

PINNIDAE Leach, 1819 [June]

Reference: *Journal de Physique, de Chimie, d'Histoire Naturelle et des Arts*, 88: 466

Type genus: *Pinna* Linnaeus, 1758

Remarks: -inae [as -ana], Bronn (1862: 474, 499); -oidea [as -acea], Eberzin (1960: 79).

PINZONELLIDAE Beurlen, 1954 [19 December]

Reference: *Paleontologia do Parana*: 121

Type genus: †*Pinzonella* Reed, 1932

PIRONAEIDAE Yanin, 1990

Reference: [in Menner, ed.] *Sistematika i filogeniia bespozvonochnykh. Kriterii vydeleniia vyschikh taksonov*: 67

Type genus: †*Pironaea* Meneghini, 1868

Remarks: Original spelling Pironaeidea.

PISIDIIDAE Gray, 1857

Reference: [New edition, with additions, of W. Turton] *Manual of the land and fresh-water shells of the British Islands*: 263

Type genus: *Pisidium* C. Pfeiffer, 1821

Remarks: Original spelling Pisidiadae. Also published by Gray (1857b: 34). Placed on the Official List by Direction 27 (1955: 483, 485). -inae, F.C. Baker (1927: 220); -oidea, Nevesskaja et al. (1971: 16).

PITARINAE Stewart, 1930 [9 August]

Reference: *The Academy of Natural Sciences of Philadelphia. Special Publication*, 3: 215, 232

Type genus: *Pitar* Römer, 1857

PLACENTIDAE Gray, 1847 [November]

Reference: *Proceedings of the Zoological Society of London*, 15: 201

Type genus: *Placenta* Philipsson, 1788

Remarks: Original spelling Placentadae. -inae [as "Trib." Placentadae, below family Ostracea], Mörch (1853: 62).

PLACUNANOMIINAE Beu, 1967 [2 November]

Reference: *Transactions of the Royal Society of New Zealand, Zoology*, 9(18): 228

Type genus: *Placunanomia* Broderip, 1832

PLACUNINAE Rafinesque, 1815

Reference: *Analyse de la nature*: 148

Type genus: *Placuna* Lightfoot, 1786

Remarks: Original spelling Placunia. -idae, Gray (1840b: 142, 151). Again proposed as a "new family" by Yonge (1977: 516).

PLACUNOPSIDAE Freneix, 1985

Reference: [in Freneix et al.] *Bulletin Trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre*, 72(4): 30

Type genus: †*Placunopsis* J. Morris & Lycett, 1853

PLAGIOPTYCHINAE Douvillé, 1888

Reference: *Bulletin de la Société Géologique de France*, ser. 3, 16: 725, 729

Type genus: †*Plagioptychus* Matheron, 1842

Remarks: Original spelling (subfamily) "Plagioptychinés" (vernacular). Latinized by MacGillavry (1937: 104, 105, 153). -idae, Bobkova & Pchelintsev (in Eberzin, 1960: 159), who explicitly attributed the name to Douvillé, 1888.

PLAGIOSTOMINAE Kasum-Zade, 2003

Reference: [Advance in research of Mesozoic bivalve mollusks in Azerbaijan Order Pectinoida: revision and systematics]: 60, 87

Type genus: †*Plagiostoma* J. Sowerby, 1814

PLANACARDIINI Paramonova, 2001

Reference: [in Nevesskaja, Paramonova & Popov] *Paleontological Journal*, 35, supplementary issue 3: 149, 181

Type genus: †*Planacardium* Paramonova, 1971.

Remarks: -ina, Bieler, Carter & Coan, herein.

PLEIODONTIDAE Rochebrune, 1904

Reference: *Bulletin du Muséum d'Histoire Naturelle* [Paris], 10(6): 342

Type genus: *Pleiodon* Conrad, 1834

Remarks: Original spelling Pliodontidae, based on *Pliodon*, an incorrect subsequent spelling of *Pleiodon*. -inae [as Pleiodoninae, declared new], Pain & Woodward (1964: 5).

PLESIOCYPRINELLINAE Simões, Marques, de Mello & Anelli, 1997

Reference: *Journal of Comparative Biology*, 2(2): 83

Type genus: †*Plesiocyprinella* Holdhaus, 1919

Remarks: Independently declared new by Waterhouse (2001: 147).

PLESIODICERATIDAE Pchelintsev, 1959

Reference: *Rudisty Mezozoya Gornogo Kryma*: 36

Type genus: †*Plesiodiceras* Munier-Chalmas, 1882

Remarks: -inae, Coogan (in Moore, ed., 1969: 779).

PLETHOCARDIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 22, 32

Type genus: †*Plethocardia* Ulrich, 1892

PLEURIOCARDIINAE Schneider, 1995

Reference: *Zoologica Scripta*, 24(4): 346

Type genus: †*Pleuriocardia* Scott, 1978

PLEUROBEMINAE Hannibal, 1912

Reference: *Proceedings of the Malacological Society of London*, 10(2): 118–120

Type genus: *Pleurobema* Rafinesque, 1819

Remarks: Independently declared new by Modell (1942: 179). -ini, J. B. Burch (1975: 2).

PLEURODESMATIDAE Cossmann, 1909 [13 November]

Reference: [in Cossmann & Peyrot] *Actes de la Société Linnéenne de Bordeaux*, 63(3): 187

Type genus: †*Pleurodesma* M. Hörnes, 1859

Remarks: -oidea, Nevesskaja et al. (1971: 18).

PLEURODONTINAE Conrath, 1887 [14 July]

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 96(1): 49

Type genus: †*Pleurodonta* Conrath, 1887

Remarks: Invalid: type genus a junior homonym of *Pleurodonta* Herrmannsen, 1847 [itself an unjustified emendation of *Pleurodonte* Fischer von Waldheim, 1807].

PLEUROMYIDAE Zittel, 1895

Reference: *Grundzüge der Paläontologie (Paläozoologie)*: 304

Type genus: †*Pleuromya* Agassiz, 1843

Remarks: -oidea, Scarlato & Starobogatov (1979a: 22).

PLEUROPHORIDAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 538

Type genus: †*Pleurophorus* King, 1844

Remarks: -inae, same reference. Invalid: type genus a junior homonym of *Pleurophorus* Mulsant, 1842 [Coleoptera]; see Permophoridae.

PLEUOTRIGONIINAE van Hoepen, 1929

Reference: *Paleontologische Navorsing van die Nasionale Museum*, 1(1): 33

Type genus: †*Pleurotrigonia* van Hoepen, 1929

PLICATIFORMINI Paramonova, 2001

Reference: [in Nevesskaja, Paramonova & Popov] *Paleontological Journal*, 35, supplementary issue 3: 149, 179

Type genus: †*Plicatiformes* Kojumdieva, 1969.

Remarks: -ina, Bieler, Carter & Coan, herein.

PLICATOSTYLIDAE Lupper & Packard, 1929 [30 December]

Reference: *University of Oregon Publication, Geology Series*, 1(3): 204

Type genus: †*Plicatostylus* Lupper & Packard, 1929

PLICATOUNIONIDAE Chen, 1988

Reference: [Chen Jinhua] *Advances in Science of China, Earth Sciences*, 2: 143, 145

Type genus: †*Plicatounio* Kobayashi & Suzuki, 1936

Remarks: Not available (no description) from Kobayashi (1968: 124, 133).

PLICATULIDAE Gray, 1854 [1 July]

Reference: *Annals and Magazine of Natural History*, ser. 2: 1427

Type genus: *Plicatula* Lamarck, 1801

Remarks: -inae, Watson (1930: 29, 30); -oidea [as -acea], Yonge (1975: 545).

PLIOCARDIIDAE Woodring, 1925 [20 May]

Reference: *Carnegie Institution of Washington, Publication*, 366: 147

Type genus: †*Pliocardia* Woodring, 1925

PLIODONTIDAE. See Pleiodontidae.**POLICORDIIDAE** Scarlato, 1981

Reference: *Oprideliteli po faune SSSR*, 126: 419

Type genus: *Policordia* Dall, Bartsch & Rehder, 1939

POLIDEVCIINAE Kumpera, Prantl & Růžicka, 1960

Reference: *Acta Musei Nationalis Pragae, Historia Naturalis*, ser. B, 16(1–2): 33

Type genus: †*Polidevcia* Chernyshev, 1951

Remarks: -idae, Carter (1990: 153). See also Phestiinae.

POLLICIDAE Stephenson, 1953

Reference: *United States Geological Survey Professional Paper*, 242: 94

Type genus: †*Pollex* Stephenson, 1953
 Remarks: Available under Art. 13.5 (combined description of new family and genus).

POLYCONITINAE MacGillavry, 1937
 Reference: *Geographische en Geologische Mededelingen, Physiographisch-Geologische series*, 14: 104
 Type genus: †*Polyconites* Potiez & Michaud, 1844
 Remarks: -idae, Skelton & Smith (2000: 109, 122).

POLYMESODINAE Habe, 1977
 Reference: *Systematics of Mollusca in Japan. Bivalvia and Scaphopoda*: 238
 Type genus: *Polymesoda* Rafinesque, 1820

POLYDONTA Blainville, 1824
 Reference: *Dictionnaire des Sciences Naturelles*, 32: 320
 Remarks: Taxon containing the genera *Arca*, *Pectunculus* and *Nucula*. Established as a family-group name and not available as such (not based on a genus).

PONTALMYRINI Taktakishvili, 1987
 Reference: *Sistematika i filogeniia pliotse-nykh cardiid Paratetisa*: 11, 58
 Type genus: †*Pontalmyra* Stefanescu, 1896
 Remarks: Priority over simultaneously published Pseudocatillini, Digressodacnini, Char-toconchini, and Panticapaeini determined by First Reviser action by Nevesskaja et al. (2001: S191). -ina, Bieler, Carter & Coan, herein.

POPENAIADINAE Heard & Guckert, 1970 [December]
 Reference: *Malacologia*, 10(2): 339
 Type genus: *Popenaias* Frierson, 1927
 Remarks: -ini, J. B. Burch (1975: 2).

POROLEDIDAE Scarlato & Starobogatov, 1979
 Reference: *Trudy Zoologicheskogo Instituta*, 80: 19, 25
 Type genus: *Poroleda* Hutton, 1893
 Remarks: -inae, Schileyko (1989: 94).

POROMYIDAE Dall, 1886 [September]
 Reference: *Bulletin of the Museum of Comparative Zoology*, 12(6): 195, 280
 Type genus: *Poromya* Forbes, 1844
 Remarks: -inae, P. Fischer (1887: 1168); -oidea [as -acea], Dall (1895a: 534).

PORTERIINAE Scarlato & Starobogatov, 1979 [after 26 May]
 Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 23
 Type genus: †*Porterius* B. L. Clark, 1925
 Remarks: Original spelling Poteriinae, based on “*Poterius*”, cited without author. The context indicates that *Porterius* B. L. Clark, 1925, was meant.

POSIDONIIDAE Neumayr, 1891
 Reference: *Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 58: 724
 Type genus: †*Posidonia* Bronn, 1828
 Remarks: Original spelling “Posidonomyiden” (vernacular). First latinized [as Posidonomyidae] by Grobben (1892a: 142; 1892b: 373). Spelling Posidonomyidae based on *Posidonomya* Bronn, 1834, an unjustified emendation of *Posidonia*. Corrected to Posidoniinae under Art. 35.4.1, a spelling first used by Frech (1909: 8). -oidea, Scarlato & Starobogatov (1979a: 20).

POSTLIGATIDAE Scarlato & Starobogatov, 1984
 Reference: *Malacological Review*, 17(1–2): 115
 Type genus: †*Postligata* J. A. Gardner, 1916

POTAMOCORBULINAE Habe, 1977
 Reference: *Systematics of Mollusca in Japan. Bivalvia and Scaphopoda*: 282
 Type genus: *Potamocorbula* Habe, 1955

PRAEASTARTACEA Davies, 1933 [15 November]
 Reference: *Proceedings of the Malacological Society of London*, 20(6): 323
 Remarks: Latinization of “Préastartidés” of Douvillé (1912: 1681, 1682), established for a grade of Praeheterodonta, containing the genera *Prosocoelus*, *Desertella*, and *Megalodon*. Not available: not based on a genus.

PRAECARDIIDAE R. Hoernes, 1884
 Reference: *Elemente der Palaeontologie (Paleozoologie)*: 236
 Type genus: †*Praecardium* Barrande, 1881
 Remarks: Original spelling Praecardidae. -inae, Conrath (1887: 49); -oidea, Eberzin (1960: 110).

PRAEGONIINAE C. Fleming, 1962 [April]
 Reference: *Proceedings of the Malacological Society of London*, 35(1): 1
 Type genus: †*Praegonia* C. Fleming, 1962

PRAELAMELLODONTIDAE Zhang, 1980

Reference: *Bulletin of the Chinese Academy of Geological Sciences*, Series 8, 1(1): 7

Type genus: †*Praelamellodonta* Zhang, 1980

Remarks: -oidea [as -acea], same reference.

"Specimens of *Praelamellodonta* [...] are distorted valves of inarticulate brachiopods" (Pojeta, 2001: 161).

PRAELUCINIDAE Conrath, 1887 [14 July]

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 96(1): 49

Type genus: †*Praelucina* Barrande, 1881

Remarks: Precedence of simultaneously established Dualinidae determined by First Reviser action, J. Kříž (pers. com.), herein.

PRAENUCULIDAE McAlester, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 229

Type genus: †*Praenucula* Pfab, 1934

Remarks: -inae, Sánchez (1999: 67).

PRAEOSTREIDAE Kříž, 1966

Reference: *Casopis Narodniho Muzea*, 135: 28

Type genus: †*Praeostrea* Barrande, 1881

PRASINIDAE Stoliczka, 1871 [1 March]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, Vol. 3, Parts 5–8: 359

Type genus: *Prasina* Deshayes, 1863

Remarks: Established as a family of bivalves, but now classified as gastropods (see Bouchet & Rocroi, 2005: 260).

PRILUKIELLIDAE Starobogatov, 1970

Reference: *Fauna molljuskov i zoogeograficheskoe rajonirovanie kontinentalnykh vodoemov zemnogo shara*: 59

Type genus: †*Prilukiella* Plotnikov, 1945

Remarks: -inae, Betekhtina, Starobogatov & Jatsuk (1987: 44).

PRIONOPLEURINI Taktakishvili, 1987

Reference: *Sistematika i filogeniia pliotsenykh cardiid Paratetisa*: 12, 162

Type genus: †*Prionopleura* Eberzin, 1949

Remarks: -ina, Bieler, Carter & Coan, herein.

PRISODONTINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 174

Type genus: *Prisodon* Schumacher, 1817

Remarks: -idae, Morretes (1949: 17); -ini, Parodiz & Bonetto (1963: 201, 205).

PRISODONTOPSINAE Pain & F. R. Woodward, 1968 [29 March]

Reference: *Revue de Zoologie et de Botanique Africaines*, 77(1–2): 206

Type genus: *Prisodontopsis* Tomlin, 1928

Remarks: Original spelling Prisodonopsinae. *Prisodontopsis* is a replacement name for *Pseudavicula* Simpson, 1900, non Hudleston, 1890, and Prisodontopsinae was introduced as a replacement for Pseudaviculinae Modell, 1942, based on *Pseudavicula* Simpson; Art. 40 does not apply. See also Dentaspathariinae.

PRISTIGLOMIDAE Sanders & Allen, 1973 [July]

Reference: *Bulletin of the Museum of Comparative Zoology*, 145(5): 239

Type genus: *Pristigloma* Dall, 1900

Remarks: -oidea / -inae, Schileyko (1989: 93).

PROCOPIEVSKIIDAE Ragozin, 1933

Reference: *Sbornik po geologii Sibiri, posvjashchennyj 25emy jubileju nauchno-pedagogicheskoy dejatel'nosti Prof. M. A. Usova*: 314

Type genus: †*Procopievskia* Ragozin, 1933

Remarks: Not available: type genus not an available name (no type species designated). See also Prokopievskiidae.

PROFRAGINAE Badve, 1977 [March]

Reference: *Biovigyanam*, 3(1): 61

Type genus: †*Profragum* Badve, 1977

PROFULVIINI Kafanov & Popov, 1977

Reference: *Paleontologicheskii Zhurnal*, 1977(3): 62

Type genus: †*Profulvia* Kafanov, 1976

PROKOPIEVSKIIDAE H. A. Vokes, 1967 [16 June]

Reference: *Bulletins of American Paleontology*, 51(232): 201

Type genus: †*Prokopievskia* Khalfin, 1950

Remarks: Original spelling Procopievskiidae. *Procopievskia* Ragozin, 1933, is not an available name and Prokopievskiidae Ragozin,

1933, is not available. The genus name was made available as *Prokopievskia* Khalfin, 1950. Vokes did not provide a description for Prokopievskiidae, but it is available through the citation of Ragozin (1933) as author, as the latter provided a description for Prokopievskiidae.

PROMACRIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 21, 31

Type genus: †*Promacrus* Meek, 1871

Remarks: -inae [independently declared new], Morris, Dickins & Astafieva-Urbaitis (1991: 93).

PROMARGARITIFERINAE F. R. Woodward, 1994

Reference: [in Ziuganov, Zotin, Nezhlin & Tretia-kov] *The freshwater pearl mussels and their relationships with salmonid fish*: 57

Type genus: †*Promargaritifera* F. R. Woodward, 1994

Remarks: Clearly intended as a subfamily of Margaritiferidae, but incorrectly formed with the ending -idae. Not available: no description.

PROPEAMUSSIIDAE Abbott, 1954 [15 April]

Reference: *American seashells*: 361, 369

Type genus: †*Propeamussium* de Gregorio, 1884

Remarks: Name only, no description ["a family of its own on anatomical grounds", but characters not specified]. Available under Art. 13.2.1 through its use as a valid name (and description) by Waller (1971: 5). -inae, Habe (1977: 77).

PROPEHYRIDELLIDAE Iredale, 1934 [9 May]

Reference: *The Australian Zoologist*, 8(1): 57, 77

Type genus: *Propehyridella* Cotton & Gabriel, 1932

Remarks: -inae, same reference. Priority over simultaneously established Cucumerunioninae determined by Art. 24.1 (family vs. subfamily). See also Hyridellinae.

PROPTERINAE Hannibal, 1912

Reference: *Proceedings of the Malacological Society of London*, 10(2): 118–120

Type genus: *Proptera* Rafinesque, 1819

PROSOCOELIDAE Karczewski, 1992

Reference: *Prace Panstwowego Instytutu Geologicznego*, 140: 17, 28

Type genus: †*Prosocoelodon* Karczewski, 1992

Remarks: *Prosocoelodon* is an unjustified emendation of *Prosocoelus* Kerferstein, 1857. The family is monotypic and the genus is diagnosed, thus making Prosocoelidae an available name.

PROSODACNIDAE Keen, 1937 [March]

Reference: *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, 13(7): 11

Type genus: †*Prosodacna* Tournouër, 1882

Remarks: Name only, no description. Available through its use as a valid name, e.g. by Keen (in Moore, ed., 1969: 591). -inae, Andreescu (1974: 130, declared new); -ini, Kafanov & Popov (1977: 60).

PROSGYROTRIGONIINAE Kobayashi, 1954

Reference: *Japanese Journal of Geology and Geography, Transactions*, 25(1–2): 63

Type genus: †*Prosogyrotrigonia* Krumbeck, 1924

PROSPONDYLIDAE Pchelintseva, 1960

Reference: [in Eberzin] *Osnovy Paleontologii. Molljuskii. Pantsirnye, Dvustvorchatye, Lopatonogie*: 86

Type genus: †*Prospondylus* Zimmermann, 1886

PROTHYRIDAE S. A. Miller, 1889 [after October]

Reference: *North American geology and paleontology*: 458

Type genus: †*Prothyris* Meek, 1869

Remarks: Established independently by Muromzeva & Guskov (1984: 114).

PROTOCOLIDAE Reuss, 1846

Reference: *Die Versteinerungen der böhmischen Kreideformation*, Abt. 2: 22

Type genus: †*Protocardia* Beyrich, 1845

Remarks: Original spelling Protocardidae. -inae [declared new], Keen (1951: 7).

PROTOCUSPIDARIIDAE Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 12

Type genus: *Protocuspida* Allen & Morgan, 1981

Remarks: -oidea, same reference.

PROTOENTOLIINAE Romanov, 1985

Reference: *Jurskie pectinoidy Juga SSSR*: 33

Type genus: †*Protoentolium* Janishevskii, 1960

Remarks: Not available (no description) from Romanov (1984: 84).

PROTOMYIDAE Neumayr, 1891

Reference: *Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 58: 724

Type genus: †*Protomya* Hall, 1885

Remarks: Original spelling "Protomyiden" (vernacular). First latinized by Grobben (1892a: 142; 1892b: 373). Independently declared new by Scarlato & Starobogatov (1979a: 21, 31).

PSAMMOBIIDAE J. Fleming, 1828 [March]

Reference: *A history of British animals*: 437, 440

Type genus: *Psammobia* Lamarck, 1818

Remarks: Original spelling Psammobiadae. -inae, E. A. Smith (1885: 90). Placed on the Official List by Opinion 910 (1970: 16).

PSEUDAMUSSIINAE F. Nordsieck, 1969 [October]

Reference: *Die europäischen Meeresmuscheln (Bivalvia)*: 46

Type genus: *Pseudamussium* Mörch, 1853

PSEUDANODONTINAE Stadnichenko, 1984

Reference: *Fauna Ukraini*, 29. *Moliuski* (9): 66

Type genus: *Pseudanodonta* Bourguignat, 1877

Remarks: Not available (no description) from Jaeckel (1962: 208); nor from Starobogatov (1970: 68, as -inae / -ini).

PSEUDARCIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 19, 25

Type genus: †*Pseudarca* Tromelin & Lebesconte, 1875

PSEUDAVICULINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 176

Type genus: *Pseudavicula* Simpson, 1900

Remarks: Invalid: Type genus a junior homonym of *Pseudavicula* Hudleston, 1890. See *Dentaspithariinae* and *Prisodontopsinae*.

PSEUDAVICULOPECTININAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 53

Type genus: †*Pseudaviculopecten* Newell, 1938

PSEUDENTOLIINI Waller, 2006

Reference: [in Shumway & Parsons, eds.] *Scallops: Biology, ecology and aquaculture*: 8, 12

Type genus: †*Pseudentolium* Cox, 1948

PSEUDOCARDINIIDAE Martinson, 1961

Reference: *Trudy Baikalskoi Limnologicheskoi Stantsii*, 19: 173

Type genus: †*Pseudocardinia* Martinson, 1959

Remarks: -oidea, Kolesnikov (1977: 49).

PSEUDOCARDITINAE Keen, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 593

Type genus: †*Pseudocardita* Oppenheim, 1919

Remarks: Not available (no description) from Eberzin (1965: 11). Eberzin attributed the name to himself with the date 1964, probably referring to the unpublished typescript *Proceedings of the first meeting of Soviet malacology [Vsesoiuznoe soveshchanie po izucheniiu molliuskov]*, which had taken place in 1961. The foreword to the *Proceedings of the 2nd meeting* stated that the *Proceedings of the first meeting* had a very restricted circulation. They were not available in the library of the Zoological Institute in Leningrad in 1990. In his papers published after 1965, Eberzin did not refer to any paper on *Cardiidae* he would have published in 1964.

PSEUDOCATILLINI Taktakishvili, 1987

Reference: *Sistematika i filogeniia pliotsenykh cardiid Paratetisa*: 12, 102

Type genus: †*Pseudocatillus* Andrusov, 1903

Remarks: Priority of simultaneously published *Pontalmyrini* determined by First Reviser action by Nevesskaja et al. (2001: S191). -ina, Bieler, Carter & Coan, herein.

PSEUDOCLARAIINAE Gavrilova, 1996

Reference: *Paleontologicheskii Zhurnal*, 1996(4): 12

Type genus: †*Pseudoclaraia* Zhang, 1980

Remarks: -ini, n.t., Waterhouse (2000: 179).

PSEUDOCYRTODONTIDAE Maillieux, 1939 [28 February]

Reference: *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 86: 34

Type genus: †*Pseudocyrtodonta* Pfab, 1934

PSEUDODONTINAE Frierson, 1927 [April]

Reference: *A classified and annotated check list of the North American naiades*: 67

Type genus: *Pseudodon* Gould, 1844

Remarks: -ini, Starobogatov (1970: 61).

PSEUDOHYRIINAE Kobayashi, 1968

Reference: *Geology and Palaeontology of Southeast Asia*, 4: 123, 127

Type genus: †*Pseudohyria* MacNeil, 1936

Remarks: -idae, Kolesnikov (1977: 48).

PSEUDOMONOTINAE Newell, 1938 [28 July]

Reference: *State Geological Survey of Kansas Publications*, 10(1): 92

Type genus: †*Pseudomonotis* Beyrich, 1862

Remarks: -idae, Newell (1965: 18); -oidea [as -acea], Newell & Boyd (1995: 64, 65).

PSEUDOMULLERIIDAE Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinentalnykh vodoemov zemnogo shara*: 75, 288

Type genus: *Pseudomulleria* Anthony, 1907

PSEUDOPECTININAE Kasum-Zade, 2003

Reference: [Advance in research of Mesozoic bivalve mollusks in Azerbaijan Order Pectinida: revision and systematics]: 54, 85

Type genus: †*Pseudopecten* Bayle, 1878

PSEUDOPOLYCONITIDAE Sladić-Trifunović, 1983

Reference: *Annales Géologiques de la Péninsule Balkanique*, 47: 239

Type genus: †*Pseudopolyconites* Milovanovic, 1937

Remarks: Not available from Sladic-Trifunovic (1980, unpublished thesis). -inae, Morris & Skelton (1995: 278).

PSEUDOSPETHINAE Leloup, 1950 [31 December]

Reference: *Exploration Hydrobiologique du Lac Tanganyika. Résultats Scientifiques*, 3(1): 7

Type genus: *Pseudospatha* Simpson, 1900

Remarks: Name only, no description. Not available under Art. 13.2.1, unless discovery of an author who used the name before 2000.

PSEUDOTECHNOPHORIDAE Starobogatov, 1977

Reference: *Biulleten' Moskovskogo Obshchestva Ispitatelei Priroda, Otdel Geologicheskii*, 52(4): 135

Type genus: †*Pseudotechnophorus* Kobayashi, 1933

Remarks: Established as a family of bivalves, but now classified in the separate class Rostroconchia.

PSEUDOVACCINITINAE Bilotte, 1982

Reference: *Bulletin de la Société d'Histoire Naturelle de Toulouse*, 117: 111

Type genus: †*Pseudovaccinites* Sénèsse, 1946

Remarks: Original spelling (subfamily) Pseudovaccinitidae with incorrect ending.

PSILODONTINI Taktakishvili, 1987

Reference: *Sistematika i filogenija pliotsenykh cardiid Paratetisa*: 12, 159

Type genus: †*Psilodon* Cobalcescu, 1883

Remarks: Original spelling Psilodonini. Invalid: type genus a junior homonym of *Psilodon* Perty, 1830 [Coleoptera].

PSILOTRIGONIINAE C. Fleming, 1987

Reference: *New Zealand Geological Survey Paleontological Bulletin*, 53: 39

Type genus: †*Psilotrignia* Cox, 1952

PSILUNIONINAE Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinentalnykh vodoemov zemnogo shara*: 65, 284

Type genus: †*Psilunio* Stefanescu, 1896

PTERIIDAE Gray, 1847 [November] (1820)

Reference: *Proceedings of the Zoological Society of London*, 15: 199

Type genus: *Pteria* Scopoli, 1777

Remarks: Original spelling Pteriadae. -inae [as Pteriacna], Gray (1854a: 418); -oidea [as -acea], Dall (1895a: 518). When he established the name Pteriidae, Gray did not cite Aviculidae (which he [Gray, 1840b] had earlier used for the same taxon), but he cited *Avicula* as a synonym of *Pteria*. Pteriidae is in prevailing usage, and it is conserved under Art. 40 with the priority of Aviculidae (1820), a conclusion already reached by Hertlein & Cox (in Moore, ed., 1969: 302).

PTERINEINAE Meek, 1864 [May]

Reference: *The American Journal of Science and Arts*, ser. 2, 37: 217

Type genus: †*Pterinea* Goldfuss, 1832

Remarks: Original spelling Pteriniinae, based on *Pterinia*, an incorrect subsequent spelling of *Pterinea*. -idae, S. A. Miller (1877: 180); -oidea, Astafieva (1987: 111).

PTERINELLINAE Hayami, 1965 [1 March]

Reference: *Memoirs of the Faculty of Science, Kyushu University*, ser. D, Geology, 15(2): 261

Type genus: †*Pterinella* Toulou, 1882

PTERINOPECTINELLINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 46

Type genus: †*Pterinopectinella* Newell, 1938

PTERINOPECTINIDAE Newell, 1938 [28 July]

Reference: *State Geological Survey of Kansas Publications*, 10(1): 36

Type genus: †*Pterinopecten* Hall, 1883

Remarks: -oidea [as -acea], Newell & Boyd (1995: 25); -inae, Gavrilova (1996: 12).

PTEROCARDIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 22, 32

Type genus: †*Pterocardia* Bayan, 1874

PTEROCHAENIINAE Fang & Ding, 1993 [January]

Reference: [Fang Zong-jie & Ding Wei-ming] *Acta Palaeontologica Sinica*, 32(1): 4 [Chinese], 10 [English]

Type genus: †*Pterochaenia* Clarke, 1904

PTEROPSELLINAE Keen, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 605

Type genus: †*Pteropsella* H. A. Vokes, 1956

Remarks: Not available (no description) from Keen (1963: 92). Established as a substitute name for Pteropsinae, invalid because its type genus is a junior homonym. Keen gave Pteropsellinae the priority of Pteropsinae, but Art. 40.2 does not apply.

PTEROPSINAE Dall, 1894 [August]

Reference: *The Nautilus*, 8(4): 41

Type genus: †*Pteropsis* Conrad, 1860

Remarks: Invalid: Type genus a junior homonym of *Pteropsis* Rafinesque, 1814. Also spelled Pteropsidinae. See Pteropsellinae.

PTEROTRIGONIINAE van Hoepen, 1929

Reference: *Paleontologiese Navorsing van die Nasionale Museum*, 1(1): 9

Type genus: †*Pterotrigonia* van Hoepen, 1929

PTYCHOBANCHINAE Starobogatov, 1970

Reference: *Fauna molljuskov i zoogeograficheskoe rajonirovanie kontinentalnykh vodoemov zemnogo shara*: 70, 287

Type genus: *Ptychobanchus* Simpson, 1900

PTYCHODESMATIDAE Scarlato & Starobogatov, 1984

Reference: *Malacological Review*, 17: 116

Type genus: †*Ptychodesma* Hall & Whitfield, 1872

Remarks: -oidea, same reference.

PTYCHOMYIDAE Keen, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 655

Type genus: †*Ptychomya* Agassiz, 1842

Remarks: -inae, Freneix (1972: 155).

PUCAMYIDAE Sánchez, 2007 [August]

Reference: [in Sánchez & Benedetto] *Geobios*, 40(4): 530

Type genus: †*Pucamya* Sánchez, 2007

PULVINITIDAE Stephenson, 1941 [October]

Reference: *The University of Texas, Publication*, 4101: 151

Type genus: †*Pulvinites* Defrance, 1824

Remarks: Name only, no description. Diagnosed by Cox (in Moore, ed., 1969: 326), who attributed the name to Stephenson.

PUSTULOSTREINI Harry, 1985 [1 October]

Reference: *The Veliger*, 28(2): 147

Type genus: *Pustulostrea* Harry, 1985

PYCNODONTEINAE Stenzel, 1959

Reference: *Congreso Geologico Internacional*, 20 [Ciudad de Mexico, 1956]. *El sistema cretacico*, 1: 16, 29

Type genus: †*Pycnodonte* Fischer von Waldheim, 1835

Remarks: -idae, Torigoe (1981: 319); -ini, Malchus (1990: 143); -oidea, A. Ivanov (1995: 33).

PYLORIDEA Blainville, 1824

Reference: *Dictionnaire des Sciences Naturelles*, 32: 345

Remarks: Established as a family including the genera *Pandora*, *Anatina*, *Thracia*, *Mya*, *Sanguinolaria*, *Solecurtus*, *Solen*, etc. Not available as a family-group name (not based on a genus).

QIYANGIIDAE Chen, 1983

Reference: *Transactions of the Chinese Society of Malacology*, 1: 222

Type genus: †*Qiyangia* Chen & Yu, 1980

Remarks: Again declared new family by Chen (1987: 15, 16). -inae, Chen (in Fang et al., 2009: 75).

QUADRATOTRIGONIINAE Saveliev, 1958

Reference: *Trudy Vsesoiuznogo Neftianogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Instituta [VNIGRI]*, 125: 97

Type genus: †*Quadratotrighonia* Dietrich, 1933

QUADRULINAE Ihering, 1901 [3 September]Reference: *The Nautilus*, 15(5): 53Type genus: *Quadrula* Rafinesque, 1820

Remarks: -idae, Hannibal (1912: 119); -ini, Graf (2002: 69). Junior homonym of Quadrulidae Schulze, 1877 [Foraminifera], itself invalid because its type genus (*Quadrula* Schulze, 1875) is a junior homonym of *Quadrula* Rafinesque, 1820.

QUENSTEDTIIDAE Cox, 1929Reference: *Proceedings of the Dorset Natural History and Archaeological Society*, 50: 191Type genus: †*Quenstedtia* J. Morris & Lycett, 1854**RADIIDENTIDAE** Egorova & Starobogatov, 1975Reference: [in Scarlato & Starobogatov] *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 5: 4Type genus: *Radiidens* Egorova & Starobogatov, 1975

Remarks: Egorova & Starobogatov established *Radiidens* as a substitute name for “*Silicula* Thiele, 1935 [sic], non Jeffreys, 1879”, with *S. fragilis* Jeffreys, 1879, as type, while considering that *Silicula* Jeffreys was a substitute name for *Phaseolus* Monterosatus, 1875, and thus with the same type species (*P. ovatus* Monterosato, 1875). Jeffreys somewhat ambiguously established *Silicula* as a substitute name for *Phaseolus* Monterosato, 1875 (which he believed not to have been properly established and to be preoccupied in botany), while at the same time fixing *S. fragilis* Jeffreys, 1879, as type. Thiele (1934) explicitly attributed *Silicula* to Jeffreys, 1879, and stated the type species to be *S. fragilis* Jeffreys, 1879. Allen & Sanders (1973) cited *S. fragilis* as type of *Silicula* when they established the name Siliculidae. Depending on the valid type species of *Silicula*, Siliculidae is either an objective synonym of Phaseolidae or a potentially valid name with Radiidentidae as an objective synonym. Under Art. 65.2, the case should be brought to the Commission. -oidea, same reference.

RADIOLAEWELLINAE A. Ivanov, 1995Reference: *Paleontologicheskii Zhurnal*, 1995(3): 34Type genus: †*Radiolaewella* A. Ivanov, 1995**RADIOLITIDAE** d'Orbigny, 1847Reference: *Comptes Rendus Hebdomadaires de l'Académie des Sciences*, 25: 269Type genus: †*Radiolites* Lamarck, 1801

Remarks: Original spelling Radiolidae, spelling corrected by Gray (1848: 439). -inae, MacGillavry (1937: 37); -oidea, Yanin (1990: 66). Priority over simultaneously published Caprinidae determined by First Reviser action by Bouchet & Rocroi, herein.

RADULIDAE H. Adams & A. Adams, 1858 [January]Reference: *The Genera of Recent Mollusca*, 2: 556Type genus: *Radula* Mörch, 1853**RADULOPECTININAE** Romanov, 1985Reference: *Iurskie pectinoidy Iuga SSSR*: 111Type genus: †*Radulopecten* Rollier, 1911

Remarks: Not available from Romanov (1984: 85), where the name is proposed without description, and attributed in error to Rollier, 1911.

RAETOMYIDAE Newton, 1919 [16 April]Reference: *Proceedings of the Malacological Society of London*, 13(3–4): 81Type genus: †*Raetomya* Newton, 1919**RAMONALINIDAE** Yancey, M. A. Wilson & Mione, 2009 [13 November]Reference: *Palaeontology*, 52(6): 1351Type genus: †*Ramonalina* Yancey, M. A. Wilson & Mione, 2009**RANGIIDAE** P. Fischer, 1884 [17 October]Reference: *Journal de Conchyliologie*, 32(2): 118Type genus: *Rangia* des Moulins, 1832

Remarks: Established as a replacement name for Gnathodontidae, based on *Gnathodon*, treated by Fischer as a synonym of *Rangia*. Gnathodontidae and Rangiidae were both established in 1884, and Art. 40.2 does not change the year of priority of Rangiidae.

RECTIDENTINAE Modell, 1942 [15 October]Reference: *Archiv für Molluskenkunde*, 74(5–6): 189Type genus: *Rectidens* Simpson, 1900

Remarks: Priority over simultaneously published Contradentinae determined by First Reviser action by Brandt (1974: 287). -ini, Graf (2002: 66).

REDONIIDAE Babin, 1966Reference: *Mollusques Bivalves et Céphalopodes du Paléozoïque armoricain*: 243Type genus: †*Redonia* Rouault, 1851

RENIELLIDAE Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 230

Type genus: *Reniella* Swainson, 1840

Remarks: Name only, no description. Available under Art. 13.2.1 because it has been used as a valid name before 2000 (e.g., Cotton 1961: 73).

REQUIENIIDAE Kutassy, 1934 [31 December]

Reference: *Fossilium Catalogus*, I, Pars 68: 4

Type genus: †*Requienia* Matheron, 1842

Remarks: Original spelling Requienidae. Not available from the vernacular “Réquiéniidés” of Douvillé (1914: 383). Although Kutassy did not provide a description, reference to Douvillé (who did) makes the name available. -oidea, Scarlato & Starobogatov (1979a: 22, 33). See also Bayleidae.

RESANIINAE Marwick, 1931

Reference: *New Zealand Geological Survey Palaeontological Bulletin*, 13: 73

Type genus: *Resania* Gray, 1853

Remarks: Established without description, but made available by its use as a valid name before 2000, e.g. by Beu (1966: 68).

RETHIDAE Yanin, 1990

Reference: [in Menner, ed.] *Sistematika i filogeniia bespozvonochnykh. Kriterii vydeleniia vyschikh taksonov*: 66

Type genus: †*Retha* Cox, 1965

RETROCERAMIDAE Koschelkina, 1980

Reference: *Ekosistemi v stratigrafii*: 132

Type genus: †*Retroceramus* Koschelkina, 1959

Remarks: Not available (no description) from Pergament (1969: 33); nor from Koschelkina (1971: 44).

RHIPIDODONTINI Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 72

Type genus: *Rhipidodonta* Mörch, 1853

Remarks: Established as a replacement name for Diplodontinae Ihering, 1901 [based on *Diplodon* Spix, 1827], homonym of Diplodontidae Carpenter, 1861 [based on *Diplodonta* Bronn, 1831].

RHOMBOPTERIIDAE Korobkov, 1960

Reference: [in Eberzin] *Osnovy Paleontologii. Molliuski. Pantsirnye, Dvustvorchatye, Lopatonogie*: 81

Type genus: †*Rhombopteria* Jackson, 1890

Remarks: -oidea [in synonymy of Leiopectinoidea], Nevesskaja (2003: 616).

RIBEIRIIDAE Kobayashi, 1933

Reference: *Journal of the Faculty of Science, Imperial University of Tokyo, section 2*, 3(7): 282, 309

Type genus: †*Ribeiria* Sharpe, 1853

Remarks: Original spelling Ribeiridae. -inae, same reference. Established as a family of bivalves, but now included in the separate class Rostroconchia.

ROCELLARIIDAE Ridewood, 1903 [31 January]

Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 187, 258

Type genus: *Rocellaria* Blainville, 1828

ROUSSELIINAE MacGillavry, 1937

Reference: *Geographische en Geologische Mededelingen, Physiographisch-Geologische series*, 14: 46, 106

Type genus: †*Rousselia* Douvillé, 1898

RUDISTIDAE Lamarck, 1818

Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 424

Remarks: Original spelling “Les Rudistes” (vernacular). Latinized, as (family) Rudista, by Children (1823: 46); and, as Rudistidae, by Broderip (1839: 320). Ranked as superfamily Rudistae by Dall (1895a: 543). Not available as a family-group name (not based on a genus). See also higher categories list.

RUTITRIGONIINAE van Hoepen, 1929

Reference: *Paleontologiese Navorsing van die Nasionale Museum*, 1(1): 31

Type genus: †*Rutitrigonia* van Hoepen, 1929

Remarks: -idae, M. R. Cooper (1991: 24).

RZEHAKIIDAE Korobkov, 1954

Reference: *Spravochnik i metodicheskoe rukovodstvo po tretichnym molliuskam*: 168

Type genus: †*Rzehakia* Korobkov, 1954

Remarks: When he established Rzehakiidae, Korobkov did not cite Oncophoridae, but he established *Rzehakia* as a substitute name for *Oncophora* Rzehak, 1882, non Diesing, 1851. Art. 40.2 does not apply.

SACHALINOCERAMINAE Zonova, 1984

Reference: [in Pojarkova, ed.] *Novye dannye po detalnoi biostratigrafii Fanerozoia Dalnego Vostoka*: 116

Type genus: †*Sachalinoceras* Glasunov, 1967

SAFFORDIIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 20, 26

Type genus: †*Saffordia* Ulrich, 1894

Remarks: Original spelling Safforidiidae, based on *Safforidia*, an incorrect subsequent spelling.

SAHAROPTERIIDAE G. Termier & H. Termier, 1972 [December]

Reference: [in Pareyn et al.] *Annales de la Société Géologique du Nord*, 91(4): 233

Type genus: †*Saharopteria* G. Termier & H. Termier, 1972

SAIKRACONCHINAE Yancey & Ozaki, 1986 [4 February]

Reference: *Journal of Paleontology*, 60(1): 120

Type genus: †*Saikraconcha* Yancey & Boyd, 1983

SAINSCHANDIIDAE Kolesnikov, 1977

Reference: *Paleontologicheskii Zhurnal*, 1977(3): 48

Type genus: †*Sainschandia* Martinson, 1961

Remarks: Original spelling Sainshandiidae, based on *Sainshandia*, an incorrect subsequent spelling of *Sainschandia*. Attributed by the author to "Kolesnikov, 1974", but we could not locate the name in any of Kolesnikov's papers prior to 1977.

SAMARANGIINAE Keen, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 679

Type genus: *Samarangia* Dall, 1902

SANCTICAROLITIDAE Simone & Mezzalira, 1997

Reference: *Geociencias [Universidade Garulhos, Brazil]*, 2(6): 64

Type genus: †*Sancticarolis* Mezzalira, 1974

Remarks: Not available (no description) from Simone & Mezzalira (1994: 76).

SANGUINOLARIIDAE M. Smith, 1937

Reference: *East coast marine shells*, ed. 1: 63

Type genus: *Sanguinolaria* Lamarck, 1799

Remarks: First published without description by Grant & Gale (1931: 381), and rejected under Art. 13a by Coan, Scott & Bernard (2000: 424). -inae, Franc (1960: 2114).

SANGUINOLITIDAE S. A. Miller, 1877

Reference: *The American Palaeozoic fossils*: 180

Type genus: †*Sanguinolites* M'Coy, 1844

SAREPTINAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8c

Type genus: *Sarepta* A. Adams, 1860

Remarks: A. Adams (1860: 302) suggested that *Sarepta* "belongs to a distinct subfamily between Nuculinae and Malletiinae", but did not formally name it. -idae / -oidea, Scarlato & Starobogatov (1979a: 19, 25).

SATURNELLINAE Astafieva, 1994

Reference: *Paleontological Journal*, 28(1A): 12, 16

Type genus: †*Saturnella* Astafyeva, 1994

SATURNIIDAE Allen & Hannah, 1986 [November]

Reference: *Journal of Conchology*, 32(4): 230

Type genus: †*Saturnia* Seguenza, 1877

Remarks: Invalid: Type genus a junior homonym of *Saturnia* Schrank, 1802 [Lepidoptera]. See Neilonellinae.

SAUVAGESIIDAE Wiontzek, 1934 [February]

Reference: *Palaeontographica*, Abt. A, 80: 1, 26

Type genus: †*Sauvagesia* Choffat, 1886

Remarks: Original spelling Sauvagesinidae. Established without description, but made available by its use as a valid name before 2000, e.g. by Dechaseaux & Coogan (in Moore, ed., 1969: 810, as -inae, n.t.). Under Art. 11.7.2, not available from the vernacular "Sauvagésinés" of Douvillé (1910: 24, 28).

SAXICAVELLINAE Scott, 1994 [3 January]

Reference: *The Veliger*, 37(1): 63

Type genus: *Saxicavella* P. Fischer, 1878

SAXICAVIDAE Swainson, 1835

Reference: *The elements of modern conchology*: 30

Type genus: *Saxicava* Fleuriau-Bellevue, 1802

Remarks: -oidea [as -acea], Haas (1929: 18).

SCABROTRIGONIINI M. R. Cooper, 1989 [December]

Reference: *Paläontologische Zeitschrift*, 63(3–4): 243

Type genus: †*Scabrotrigonia* Lebküchner, 1932

SCACCHIIDAE Récluz, 1869

Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): unnumbered table between pp. 34 and 35

Type genus: *Scacchia* Philippi, 1844

Remarks: Original spelling Scacchiadae. -inae [established independently], Glibert & van de Poel (1967: 53).

SCAMBULINAE Chavan, 1952 [23 October]

Reference: *Cahiers Géologiques de Thoiry*, 14: 120

Type genus: †*Scambula* Conrad, 1869

SCAPHELLINIDAE Newell & Ciriacks, 1962 [28 December]

Reference: *American Museum Novitates*, 2121: 2

Type genus: †*Scaphellina* Newell & Ciriacks, 1962

SCAPHULINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25

Type genus: *Scaphula* Benson, 1834

SCHIZODIDAE Newell & Boyd, 1975 [3 January]

Reference: *Bulletin of the American Museum of Natural History*, 154: 94

Type genus: †*Schizodus* King, 1845

Remarks: -inae, M. R. Cooper (1991: 4). Precedence over simultaneously published Eoastartidae determined by First Reviser action by Boyd & Newell (1997: 6).

SCINTILLIDAE Iredale & McMichael, 1962

Reference: *The Australian Museum, Sydney. Memoir*, 11: 21

Type genus: *Scintilla* Deshayes, 1856

Remarks: Not available: name only, no description.

SCROBICULARIINAE H. Adams & A. Adams, 1856 [November]

Reference: *The Genera of Recent Mollusca*, 2: 408

Type genus: *Scrobicularia* Schumacher, 1815

Remarks: -idae, Stoliczka (1870: 106); -oidea, Nevesskaja et al. (1971: 18).

SELENIMYALININAE Weyer, 1968

Reference: *Geologie* [Berlin], 17(5): 566

Type genus: †*Selenimyalina* Newell, 1942

SEMELINAE Stoliczka, 1870 [1 September] (1825)

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b, 106, 108

Type genus: *Semele* Schumacher, 1817

Remarks: -idae, Tryon (1884: 162). When he established Semelinae, Stoliczka treated *Amphidesma* as a synonym of *Semele*; Semelidae is in prevailing usage and is conserved under Art. 40.2 with the priority of Amphidesmatidae (1825).

SEMI-SOLENACÉS Beltrémieux, 1864

Reference: *Faune du département de la Charente-Inférieure*: 86

Remarks: Vernacular name only. Established as a family including the genera *Saxicava* and *Pandora*. Not available: not based on a genus.

SENDERZONIELLINAE Betekhtina, Starobogatov & Jatsuk, 1987

Reference: *Akademiia Nauk SSSR, Sibirskoe Otdelnie, Institut Geologii i Geofiziki, Trudy*, 688: 44

Type genus: †*Senderzoniella* Betekhtina, 1977

Remarks: *Senderzoniella* is a replacement name for *Microdontella* Lebedev, 1944 [non Strand, 1934], which was the type genus of the invalid family name Microdontellidae.

SENILIINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25

Type genus: *Senilia* Gray, 1842

SEPTIBRANCHIA Grobben, 1892

Reference: *Arbeiten aus dem Zoologischen Institut der Universität Wien und der Zoologischen Station in Triest*, 10(2): 142 [offprint 42]

Remarks: Also published in Grobben (1892b: 373). Name established by Pelseneer (1888) above family level (see higher category list). Treated by Grobben as a family and not available as such (not based on a genus name).

SEPTIFERIDAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 25

Type genus: *Septifer* Récluz, 1848

Remarks: -inae, n.t., same reference.

SEPTOCARDIIDAE Kafanov & Starobogatov, 1977

Reference: [in Kafanov & Popov] *Paleontologicheskii Zhurnal*, 1977(3): 61

Type genus: †*Septocardia* Hall & Whitfield, 1877

SERRILAMINULINAE Lindholm, 1933

Reference: *Archiv für Molluskenkunde*, 65: 268

Type genus: *Serrilaminula* Lindholm, 1933

Remarks: Lindholm stated that the generic description is that given by Clessin for *Corbicula fluminalis*; the subfamily includes a single genus-group taxon, and its description can probably be taken as that of the genus, making Serrilaminulinae available under Art. 13.5.

SERRIPECTININI Waller, 2006

Reference: [in Shumway & Parsons, eds.] *Scallops: Biology, ecology and aquaculture*: 8, 15

Type genus: †*Serripecten* Marwick, 1928

SERRIPEDINI Kafanov, 1975

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 5: 146, 147

Type genus: *Serripes* Gould, 1841

Remarks: Priority of simultaneously established Clinocardiinae determined by Art. 24.1 (subfamily vs tribe).

SETIGLOMINAE Schileyko, 1983 [12 May]

Reference: *Biulleten' Moskovskogo Obshchestva Ispitatelei Priroda, Otdel Biologicheskii*, 88(4): 100

Type genus: *Setigloma* Schileyko, 1983

SHAANXICONCHIDAE Liu, 1980

Reference: [Liu Benpei] *Bivalve Fossils, 1, Triassic*: 6

Type genus: †*Shaanxiconcha* Liu, 1980

Remarks: Original spelling Shaanxiconchida. Combined family and genus description.

SIBIRECONCHIDAE Kolesnikov, 1977

Reference: *Paleontologicheskii Zhurnal*, 1977(3): 49

Type genus: †*Sibireconcha* Lebedev, 1958

SILICULIDAE Allen & Sanders, 1973 [July]

Reference: *Bulletin of the Museum of Comparative Zoology*, 145(6): 264

Type genus: *Silicula* Jeffreys, 1879

Remarks: See also Radiidentidae.

SILIQUINAE Bronn, 1862

Reference: *Die Klassen und Ordnungen der Weichthiere*, 3(2): 476, 502

Type genus: *Siliqua* Megerle von Mühlfeld, 1811

Remarks: Original spelling Siliquana.

SILURINIDAE Neumayr, 1891

Reference: *Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 58: 724

Type genus: †*Silurina* Barrande, 1881

Remarks: Original spelling "Siluriniden" (vernacular). First latinized by Grobben (1892a: 142; 1892b: 373).

SINISTRODONTA

See higher category list.

SINODORIDAE Pojeta & Zhang, 1984 [25 July]

Reference: *Journal of Paleontology*, 58(4): 1019

Type genus: †*Sinodora* Pojeta & Zhang, 1984

Remarks: -oidea [as -acea], Pojeta, Zhang & Yang (1986: 88).

SINOMYIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 19, 26

Type genus: †*Sinomya* Pogorevich, 1977

SINONAIINAE Chen, 1988

Reference: [Chen Jinhua] *Advances in Science of China, Earth Sciences*, 2: 143, 144

Type genus: †*Sinonaia* Guo, 1981

Remarks: Again established as subfam. nov. by Guo [Fuxiang] (1998b: 291).

SIPHONIDAE Choffat, 1886

Reference: *Recueil d'études paléontologiques sur la faune crétacique du Portugal*, 1: 29, pl. 2

Remarks: Division of bivalves (see also Siphonida in higher category list). Not available: not based on a genus.

SLAVIDAE Kříž, 1982

Reference: *Vestník Ustredniho Ustavu Geologickeho*, 57(4): 237

Type genus: †*Slava* Barrande, 1881

SOLECARDIIDAE Allan, 1950

Reference: *Australian shells*: 315

Type genus: *Solecardia* Conrad, 1849

Remarks: Name only, no description. Not available under Art. 13.2.1, unless discovery of an author who used the name before 2000.

SOLECURTIDAE d'Orbigny, 1846

Reference: *Voyage dans l'Amérique méridionale*, 5(3): 522

Type genus: *Solecurtus* Blainville, 1824
 Remarks: -inae, Ghosh (1920: 67).

SOLEMYIDAE Gray, 1840b [16 October]
 Reference: *Synopsis of the contents of the British Museum*, ed. 42: 136, 150
 Type genus: *Solemya* Lamarck, 1818
 Remarks: Original spelling Solenomyadae, based on *Solenomya*, an incorrect subsequent spelling [by Children, 1823] of *Solemya*. Solemyacidae [as used by Dall, 1896] and Solenomyacidae [as used by Dall, 1908] are incorrect subsequent spellings. First corrected to spelling Solemyidae by H. & A. Adams (1857: 481). -inae [as Solenomyana], Bronn (1862: 475, 500); -oidea [as -acea], Gill (1871: 20).

SOLENELLIDAE d'Orbigny, 1846
 Reference: *Voyage dans l'Amérique méridionale*, 5(3): 542
 Type genus: *Solenella* G. B. Sowerby I, 1833
 Remarks: Established as "Solenellidées" (vernacular) by d'Orbigny (1845: 299), but not generally cited as available from that publication. See Malletiinae.

SOLENIDAE Lamarck, 1809
 Reference: *Philosophie zoologique*: 319
 Type genus: *Solen* Linnaeus, 1758
 Remarks: Original spelling "Les solenacées" (vernacular). First latinized, as Solenacea, by Children (1822: 83), in an English translation of Lamarck's classification. -inae, Burmeister (1837: 487); -oidea [as -acea], Gill (1871: 18).

SOLENOMORPHIDAE Cockerell, 1915 [10 November]
 Reference: *The Nautilus*, 29(7): 84
 Type genus: †*Solenomorpha* Cockerell, 1903
 Remarks: Replacement name for Solenopsidae, invalid because its type genus, *Solenopsis* M'Coy, 1844, is a junior homonym.

SOLENOMYIDAE. See Solemyidae.

SOLENOPSIDAE Neumayr, 1891
 Reference: *Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 58: 724
 Type genus: †*Solenopsis* M'Coy, 1844
 Remarks: Original spelling "Solenopsiden" (vernacular). First latinized by Grobben (1892a: 142; 1892b: 373). Invalid: Type genus a junior

homonym of *Solenopsis* Westwood, 1840 [Hymenoptera]. See Solenomorphidae.

SOLETELLINIDEN Vest, 1899
 Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 143
 Type genus: *Soletellina* Blainville, 1824
 Remarks: Not available: vernacular name only, apparently never latinized

SOWERBYIDAE Cox, 1929
 Reference: *Proceedings of the Dorset Natural History and Archaeological Society*, 50: 192
 Type genus: †*Sowerbya* d'Orbigny, 1850
 Remarks: See also Isodontidae.

SPANILIDAE Kříž, 2007 [November]
 Type genus: †*Spanila* Barrande, 1881
 Reference: *Palaeontology*, 50(6): 1355, 1361

SPATHINAE Bronn, 1862
 Reference: *Die Klassen und Ordnungen der Weichthiere*, 3(2): 475, 499
 Type genus: *Spatha* I. Lea, 1838
 Remarks: Original spelling Spathana.

SPATHOPSINAE Modell, 1942 [15 October]
 Reference: *Archiv für Molluskenkunde*, 74(5–6): 176
 Type genus: *Spathopsis* Simpson, 1900
 Remarks: Precedence of simultaneously published Aspathariinae determined by First Reviser action by Graf & Cummings (2006: 394).

SPHAERIASTRINAE Alimov & Starobogatov, 1968
 Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 3: 13
 Type genus: *Sphaeriastrum* Bourguignat, 1854

SPHAERIINAE Deshayes, 1855 [12 May] (1820)
 Reference: *Catalogue of the Conchifera or bivalve shells in the collection of the British Museum, Part 2*: 261
 Type genus: *Sphaerium* Scopoli, 1777
 Remarks: Original spelling Sphaeriina. -idae, Jeffreys (1862: 1); -oidea [as -acea], Cotton & Godfrey (1938: 163, 175). Placed on the Official List by Opinion 1331 (1985: 230), where it was given the priority (1820) of Cycladidae, and attributed in error to Jeffreys, 1862; authorship and date changed to Deshayes, "1854" [in error for 1855], by Opinion 1957 (2000: 182). Sphaeriidae Erich-

son, 1845, based on *Sphaerius* Walzl, 1838 [Coleoptera], was placed on the Official Index by Opinion 1331.

SPHAEROCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 16

Type genus: †*Sphaeroceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

SPHAERULITIDÉS Douvillé, 1886

Reference: *Bulletin de la Société Géologique de France*, ser. 3, 14: 404

Type genus: †*Sphaerulites* Lamarck, 1819

Remarks: Not available: vernacular name only.

SPHENIINAE F. R. Bernard, 1983 [about 15 April]

Reference: *Canadian Special Publication of Fisheries and Aquatic Sciences*, 61: 58, 70

Type genus: *Sphenia* Turton, 1822

SPHENIOPSIDAE J. A. Gardner, 1928 [5 June]

Reference: *United States Geological Survey Professional Paper*, 142-E: 236

Type genus: †*Spheniopsis* Sandberger, 1863

SPHENOCERAMIDAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 5, 23

Type genus: †*Sphenoceramus* Böhm, 1915

Remarks: -inae, same reference.

SPINOLYONSIELLIDAE Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 10

Type genus: *Spinolyonsiella* Scarlato & Starobogatov, 1983, an objective synonym of *Allogramma* Dall, 1903.

Remarks: Scarlato & Starobogatov (1983) established *Spinolyonsiella* and *Spinolyonsiellidae* based on the description by Allen & Turner (1974) of the anatomy of a specimen identified by them as *Lyonsia formosa* Jeffreys, 1882, with reduced or absent outer demibranch. Poutiers (in Poutiers & Bernard, 1995: 169) remarked that *Lyonsia formosa* is also the type species of *Allogramma* Dall, 1903, but suggested that, under the name *Lyonsia formosa*, Dall (1903) and Allen & Turner (1974) might have treated different

taxonomic species, and concluded: “the identity of *L. formosa* (*sensu* Allen & Turner) is problematical”. However, Salas (1996) considered the gill character state described by Allen & Turner to be a juvenile feature (their specimen measured 8 mm), whereas adult *Allogramma formosa* have fully developed gills, and she retained *Allogramma* in the family Lyonsiidae. To avoid any ambiguity on the nomenclature of *Spinolyonsiella* (and *Spinolyonsiellidae*), we herewith under Art. 70.3 of the Code fix the nominal species *Lyonsia formosa* Jeffreys, 1882, as the type species of *Spinolyonsiella*.

SPINULINAE Allen & Sanders, 1982 [12 January]

Reference: *Bulletin of the Museum of Comparative Zoology*, 150(1): 2

Type genus: *Spinula* Dall, 1908

Remarks: Invalid: Type genus a junior homonym of *Spinula* Herrich-Schaeffer, 1856 [Lepidoptera]. See also Bathyspinulinae.

SPIRODOMIDAE S. A. Miller, 1889 [after October]

Reference: *North American geology and palaeontology*: 458

Type genus: †*Spirodomus* Beecher, 1886

Remarks: Probably not a mollusk according to Newell (in Moore, ed., 1969: 868).

SPONDYLIDAE Gray, 1826 [November]

Reference: *The Annals of Philosophy*, new ser., 12(5): 104, 105

Type genus: *Spondylus* Linnaeus, 1758

Remarks: -inae [as -ana], Bronn (1862: 474, 498); -oidea, Nevesskaja et al. (1971: 15). Senior homonym of Spondylidae Serville, 1832, based on *Spondylis* Fabricius, 1775 [Coleoptera].

SPONDYLOPECTINIDAE Kasum-Zade & Romanov, 1987

Reference: *Stratigrafiia verkhnego Fanerozoia Moldavii*: 7

Type genus: †*Spondylopecten* Roeder, 1882

Remarks: -oidea [as -acea] and -inae, Kasum-Zade (2003: 56, 86).

SPORELLIDAE Dall, 1899 [26 June]

Reference: *Proceedings of the United States National Museum*, 21: 875

Type genus: †*Sportella* Deshayes, 1858

SPYRIDOPECTININAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 76

Type genus: †*Spyridopecten* Campbell & McKelvey, 1972

SQUAMULIFERIPECTININAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 83

Type genus: †*Squamuliferipecten* Waterhouse, 1986

STEFANINIELLIDAE Tavani, 1939

Reference: *Palaeontographia Italica*, 39: 93

Type genus: †*Stefaniniella* Tavani, 1939

STEINMANELLINAE M. R. Cooper, 1991 [February]

Reference: *Annals of the South African Museum*, 100(1): 14

Type genus: †*Steinmanella* Crickmay, 1930

STOLIDOTIDAE Starobogatov, 1977

Type genus: †*Stolidotus* Hede, 1915

Reference: *Biulleten' Moskovskogo Obshchestva Ispitatelei Priroda, Otdel Geologicheskii*, 52(4): 135

References: Independently declared new by Kříž (2007: 1355, 1361).

STOLLEYICERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 17

Type genus: †*Stolleyiceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

STRABINAE Prantl & Růžicka, 1954

Reference: *Sbornik Narodního Musea v Praze*, 10B(3), *Geologia et Palaeontologia*, 2: 10

Type genus: †*Straba* Prantl & Růžicka, 1954

STREBLOCHONDRIINAE Newell, 1938 [28 July]

Reference: *State Geological Survey of Kansas Publications*, 10(1): 80

Type genus: †*Streblochondria* Newell, 1938

Remarks: -idae, Nevesskaja et al. (1971: 15).

STREBLOPTERIINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 106

Type genus: †*Streblopteria* M'Coy, 1851

STRIARCINAE MacNeil, 1937 [15 November]

Reference: *Journal of the Washington Academy of Sciences*, 27(11): 458

Type genus: †*Striarca* Conrad, 1862

Remarks: Name only, no description. Available through its use as a valid name, e.g. by Newell (in Moore, ed., 1969: 262).

STRIGILLINAE Habe, 1977

Reference: *Systematics of Mollusca in Japan. Bivalvia and Scaphopoda*: 207

Type genus: *Strigilla* Turton, 1822

Remarks: Not available (no description) from Iredale & McMichael (1962: 24).

STRIOSTREINI Harry, 1985 [1 October]

Reference: *The Veliger*, 28(2): 149

Type genus: *Striostrea* Vialov, 1936

STROPHITINAE Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinentalnykh vodoemov zemnogo shara*: 69, 287

Type genus: *Strophitus* Rafinesque, 1820

Remarks: -ini, Gordon (1980: 58).

STYLODACNINAE Papaianopol, 1987

Reference: *Institutul de Geologie si Geofizica, Dari de Seama ale Sedintelor*, 72–73 (3, *Paleontologie*): 110

Type genus: †*Stylodacna* Stefanescu, 1896

SUBMYTILACEA Blainville, 1824

Reference: *Dictionnaire des Sciences Naturelles*, 32: 323

Remarks: Taxon containing *Anodonta*, *Unio* and *Cardita*. Established as a family-group name and not available as such (not based on a genus).

SUBOSTRACEA Blainville, 1824

Reference: *Dictionnaire des Sciences Naturelles*, 32: 310

Remarks: Taxon containing the genera *Spondylus*, *Plicatula*, *Hinnites*, *Pecten*, *Pedum* and *Lima*. Established as a family-group name and not available as such (not based on a genus).

SUBULATACHLAMYDINAE Romanov, 1984

Reference: *Vsesoiuznogo soveshchaniia po teme "Morfologiya, sistematika, filogeniya i ekologiya dvustvorchatykh molliuskov"*: 85

Type genus: *Subulatachlamys* "Romanov, 1984"

Remarks: Original spelling *Subulatochlamydiae*. Not available: name only, no diagnosis, and type genus not then an available name. Genus name *Subulatachlamys* subsequently made available by Romanov, 1985, but this leaves *Subulatachlamydiae* unavailable because Romanov did not mention the subfamily name in 1985.

SUNETTINAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b, 153

Type genus: *Sunetta* Link, 1807

Remarks: -idae [declared new], Frizzell (1936a: 415).

SYNCYCLONEMATIDAE Waller, 1978 [16 November]

Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 284: 353

Type genus: †*Syncyclonema* Meek, 1864

Remarks: Original spelling Syncyclonemidae. -inae, Waller (2006b: 314, 325).

SYROTRIGONIINAE Pérez & Reyes, 1997 [30 December]

Reference: *Revista Geologica de Chile*, 24(2): 249

Type genus: †*Syrotrigonia* Cox, 1952

TACTOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 21

Type genus: †*Tactoceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

TAENIOCERAMINAE Aliev, 1958

Reference: *Congreso geologico internacional*, 20 [Ciudad de Mexico, 1956], section 7: 134

Type genus: †*Taenioceramus* Heinz, 1932

Remarks: Not available: no description, and type genus not an available name under Art. 13.1.1 (no description).

TANAODONTIDAE Liu, 1976

Reference: [in Gu et al.] *Fossil lamellibranchs of China*: 30

Type genus: †*Tanaodon* Kirk, 1927

Remarks: Established independently by Scarlato & Starobogatov (1979a: 20, 27).

TANCREDIIDAE Meek, 1864 [April]

Reference: *Smithsonian Miscellaneous Collections*, 7(177): 13, 33

Type genus: †*Tancredia* Lycett, 1850

TANYSIPHONIDAE Scarlato & Starobogatov, 1971

Reference: [in Nevesskaia et al.] *Paleontologicheskii Zhurnal*, 1971(2): 18

Type genus: *Tanysiphon* Benson, 1858

TAPETINAE Gray, 1851

Reference: *List of the specimens of British animals in the collection of the British Museum. Part 7, Mollusca Acephala and Brachiopoda*: 9

Type genus: *Tapes* Megerle von Mühlfeld, 1811

Remarks: Original spelling Tapesina. -idae [as Tapesidae], Récluz (1869: table between pp. 34 and 35).

TASELASMODINAE Fang & Cope, 2008 [September]

Reference: *Alcheringa*, 32(3): 299

Type genus: †*Taselasmodum* Guo, 1985

TECHNOPHORIDAE S. A. Miller, 1889 [after October]

Reference: *North American geology and palaeontology*: 458

Type genus: †*Technophorus* S. A. Miller, 1889

Remarks: -oidea, Starobogatov (1977: 137). Established as a family of bivalves, but now included in the separate class Rostroconchia.

TELLINIDAE Blainville, 1814 [2 November]

Reference: *Bulletin des Sciences par la Société Philomatique de Paris, Zoologie*, (1814): 179

Type genus: *Tellina* Linnaeus, 1758

Remarks: Original spelling “les tellinacées” (vernacular). First latinized [as Tellinides] by Latreille (1825: 219). Attributed to Blainville by Keen, in Moore (ed., 1969: 613) and H. A. Vokes (1980). -inae, Burmeister (1837: 487); -oidea [as -acea], Dall (1895a: 553).

TEREDINIDAE Rafinesque, 1815

Reference: *Analyse de la nature*: 148

Type genus: *Teredo* Linnaeus, 1758

Remarks: Original spelling Teredaria. -inae [as -ina], Mörch (1853: 2). Spelling Teredidae / -inae used by Carpenter (1861: 100) and by Tryon (1862: 192; 1863: 454, 455), to differentiate it from Teredininae based on *Teredina* (see below).

TEREDININAE Tryon, 1862 [before 1 August]

Reference: *Proceedings of the Academy of Natural Sciences of Philadelphia*, 14: 193; 454, 455 [1863]

Type genus: †*Teredina* Lamarck, 1818

Remarks: See also Teredinidae, based on *Teredo* Linnaeus.

TERQUEMIIDAE Cox, 1964 [April]

Reference: *Proceedings of the Malacological Society of London*, 36(1): 48

Type genus: †*Terquemia* Tate, 1867

TERRAIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 23, 35

Type genus: †*Terraia* Cox, 1934

TESSERATIINAE Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 49

Type genus: †*Tesseratia* Waterhouse, 2008

TETHYOCERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 10

Type genus: †*Tethyoceramus* Heinz, 1932

Remarks: Not available: type genus not an available name under Art. 13.1.1 (no description). Genus name *Tethyoceramus* subsequently made available by Sornay, 1980, but this leaves Tethyoceraminae unavailable.

THECALIINAE Dall, 1903 [20 January]

Reference: *Proceedings of the Academy of Natural Sciences of Philadelphia*, 54(4): 701

Type genus: *Thecalia* H. Adams & A. Adams, 1857

Remarks: -idae, Nevesskaja et al. (1971: 17).

THECODONTINAE F. R. Bernard, 1983 [about 15 April]

Reference: *Canadian Special Publication of Fisheries and Aquatic Sciences*, 61: 33, 68

Type genus: *Thecodonta* A. Adams, 1864

THORALIIDAE N. J. Morris, 1980

Reference: *Bulletin of the British Museum (Natural History)*, Geology Series, 34(4): 269

Type genus: †*Thoralia* N. J. Morris, 1980

THRACIINAE Stoliczka, 1870 [1 September] (1839)

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 59, 62

Type genus: *Thracia* Blainville, 1824

Remarks: -idae, Dall (1895a: 531); -oidea, Scarlato & Starobogatov (1979a: 22). When he established Thraciinae, Stoliczka did not consider the name Osteodesmatidae, and did not treat *Osteodesma* as a synonym of *Thracia*. However, *Osteodesma* Blainville,

1827, is now considered a synonym of *Thracia* and Thraciidae is in prevailing usage; it is conserved under Art. 40.2 with the priority of Osteodesmatidae (1839).

THYASIDAE Gray, 1857

Reference: *Figures of mollusious animals*, 5: 24

Type genus: *Thyas* Gray, 1857

Remarks: Invalid: type genus a junior homonym of *Thyas* Hübner, 1824 [Lepidoptera], and *Thyas* Koch, 1837 [Arachnida].

THYASIRIDAE Dall, 1900 [December] (1895)

Reference: *Transactions of the Wagner Free Institute of Philadelphia*, 5: 1116

Type genus: *Thyasira* Lamarck, 1818

Remarks: -inae, Abbott (1954: 384); and also declared new by F. R. Bernard (1983: 29, 68). *Thyasira* is a senior objective synonym of *Cryptodon*, and under Art. 40.2 Thyasiridae is conserved over Cryptodontidae with the priority of the latter (1895).

TICHOGONIIDAE Andrusov, 1893

Reference: *Zapiski Novorossiiskago Obshchestva Estestvoispytatelei*, 18(1): 71

Type genus: *Tichogonia* Rossmässler, 1835

Remarks: Original spelling Tichogonidae.

TINDARIINAE Verrill & Bush, 1897 [January]

Reference: *American Journal of Science*, 3: 58, 63

Type genus: †*Tindaria* Bellardi, 1875

Remarks: Original spelling Tindarinae. -idae, Scarlato & Starobogatov (in Nevesskaja et al., 1971: 11). Family independently declared new by Sanders & Allen (1977: 24).

TIOSTREIDAE Chanley & Dinamani, 1980

Reference: *New Zealand Journal of Marine and Freshwater Research*, 14(2): 119

Type genus: *Tiostrea* Chanley & Dinamani, 1980

TIRONUCULIDAE Babin, 1982

Reference: [in Babin et al.] *Brachiopodes et Mollusques de l'Ordovicien inférieur de la Montagne Noire*: 38

Type genus: †*Tironucula* N. J. Morris & Fortey, 1976

Remarks: -inae, Sánchez (1997: 472).

TOLMACHOVIIDAE Starobogatov, 1977

Reference: *Biulleten' Moskovskogo Obshchestva Ispitatelei Priroda, Otdel Geologicheskii*, 52(4): 138

Type genus: †*Tolmachovia* Howell & Kobayashi, 1936

Remarks: Established as a family of bivalves, but now classified in the separate class Rostroconchia.

TORREITINAE Grubic, 1979

Reference: *Zavod za Geoloska i Geofizicka Istrazivanja*, 37, ser. A (*Vesnik Geologija*): 81 [Serbo-Croatian], 90 [English]

Type genus: †*Torreites* R. H. Palmer, 1933

Remarks: Independently declared new by Bilotte (1982: 115). -idae, Philip & Platel (1994: 308, 315).

TOSAPECTININAE Trushchelev, 1984

Reference: *Trudy. Institut Geologii i Geofiziki, Sibirskoe Otdelenie, Akademii Nauk SSSR*, 600: 65

Type genus: †*Tosapecten* Kobayashi & Ichikawa, 1949

Remarks: The stem of the genus name *Pecten* is pectin- (see Introduction) and Tosapecteninae is an incorrect original spelling. -idae, Waller (2006b: 324, 328).

TOUCASIIDAE Pchelintsev, 1959

Reference: *Rudisty Mezozoa Gornogo Kryma*: 34

Type genus: †*Toucasia* Munier-Chalmas, 1873

Remarks: Name only, no description. Not available under Art. 13.2.1, unless discovery of an author who used the name before 2000.

TRACHYCARDIINAE Stewart, 1930 [9 August]

Reference: *The Academy of Natural Sciences of Philadelphia, Special Publication*, 3: 271

Type genus: *Trachycardium* Mörch, 1853

Remarks: -ini, Kafanov & Popov (1977: 59).

TRAPEZICARDIINAE Kanjilal & Srinivasan, 2002 [November]

Reference: *Journal of the Geological Society of India*, 60(5): 529

Type genus: †*Trapezicardium* Kanjilal & Srinivasan, 2002

TRAPEZIDAE Lamy, 1920 (1895)

Reference: *Journal de Conchyliologie*, 64(4): 259

Type genus: *Trapezium* Megerle von Mühlfeld, 1811

Remarks: Original spelling Trapeziidae. -oidea [as -acea], Habe (1953: 285). Established as an alternative for Cypricardiidae, probably because Lamy considered *Cypricardia* Lamarck, 1819, a synonym of *Trapezium*. Trapezidae is

in prevailing usage, and is conserved under Art. 40.2 with the priority of Cypricardiidae (1895). Placed on the Official List by Opinion 1615 (1990: 229), and spelling ruled to be Trapezidae to avoid homonymy with Trapeziidae Miers, 1886 [Crustacea].

TRECHMANNELLIDAE Cox, 1934 [15 March]

Reference: *Proceedings of the Malacological Society of London*, 21(1): 65

Type genus: †*Trechmannella* Cox, 1933

Remarks: -inae, MacGillavry (1937: 46, 106). See also Anomoptychidae and Dictyoptychidae.

TRICHOMYINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 24

Type genus: *Trichomya* Ihering, 1900

Remarks: Scarlato & Starobogatov cited *Trichomya* without author, but the context indicates that *Trichomya* Ihering, 1900, rather than *Trichomya* Crickmay, 1936, was meant.

TRIDACNIDAE Lamarck, 1819

Reference: *Histoire naturelle des animaux sans vertèbres*, 6: 102, 103

Type genus: *Tridacna* Bruguière, 1797

Remarks: Original spelling "Les Tridacnées" (vernacular). First latinized, as family Tridacnae, by Goldfuss (1820: 606); and, as Tridacnea, by Children (1823: 30). -inae [as -ana], Bronn (1862: 475, 500); -oidea [as -acea], Dall (1895a: 549).

TRIGONIIDAE Lamarck, 1819

Reference: *Histoire naturelle des animaux sans vertèbres*, 6(1): 60

Type genus: *Trigonia* Bruguière, 1789

Remarks: Original spelling "les Trigonées" (vernacular). First latinized [as Trigoniana] by Children (1823: 321), in an English translation of Lamarck's classification. Cox (in Moore, ed., 1969: 476) considered that Lamarck, 1819, had won "general acceptance" as author of Trigoniidae. -oidea [as -acea], Gill (1871: 21); -inae, Kobayashi (1954: 63).

TRIGONIOIDIDAE Cox, 1952 [9 January]

Reference: *Proceedings of the Malacological Society of London*, 29(2–3): 45

Type genus: †*Trigonioides* Kobayashi & Suzuki, 1936

Remarks: Name only, no description. Diagnosed by Cox (in Moore, ed., 1969: 488), who attributed the name to Cox, 1952. -oidea, Kolesnikov (1977: 47).

TRIGONODINAE Modell, 1942 [15 October]

Reference: *Archiv für Molluskenkunde*, 74(5–6): 179

Type genus: †*Trigonodus* Alberti, 1864

Remarks: -oidea / -idae, Nevesskaja et al. (1971: 13).

TRIGONOPINAE R. N. Gardner & H. J. Campbell, 2002 [September]

Reference: *New Zealand Journal of Geology and Geophysics*, 45(3): 335

Type genus: †*Trigonopsis* Munier-Chalmas, 1887

TRINACRIINAE MacNeil, 1937 [15 November]

Reference: *Journal of the Washington Academy of Sciences*, 27(11): 449, 458

Type genus: †*Trinacria* Mayer, 1868

TUARANGIIDAE MacKinnon, 1982 [29 April]

Reference: *Journal of Paleontology*, 56(3): 591

Type genus: †*Tuarangia* MacKinnon, 1982

Remarks: -oidea [as -acea], same reference.

TUBICOLIDAE Lamarck, 1818

Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 422, 426, 427

Remarks: Original spelling (vernacular) “Tubicolées”. Latinized by Children (1822: 79, as *Tubicolaria*); and by Broderip (1839: 319, as *Tubicolidae*). Not available as a family-group name (not based on a genus).

TULONGOCARDIINAE Schneider, 1995

Reference: *Zoologica Scripta*, 24(4): 346

Type genus: †*Tulongocardium* Chen, Chen & Zhang, 1976

TURKOSTREINI Malchus, 1990

Reference: *Berliner Geowissenschaftliche Abhandlungen*, ser. A, 125: 196

Type genus: †*Turkostrea* Vialov, 1936

TURTONIIDAE W. Clark, 1855

Reference: *A history of the British marine testaceous Mollusca*: 96

Type genus: *Turtonia* Alder, 1848

Remarks: Original spelling Turtoniadae.

TUSAYANIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 22, 32

Type genus: †*Tusayana* Stoyanow, 1948

UCUMARIIDAE Sánchez, 2003 [30 September]

Reference: [in Sánchez & Vaccari] *Ameghiniana*, 40(3): 419

Type genus: †*Ucumaris* Sánchez, 2003

UMBURRIDAE Johnston, 1991 [26 August]

Reference: *Alcheringa*, 15(3–4): 295

Type genus: †*Umburra* Johnston, 1991

Remarks: -oidea, Nevesskaja (2003: 617).

UNDOPECTININAE Waterhouse, 2001 [1 July]

Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 119

Type genus: †*Undopecten* Waterhouse, 1982

UNDULOMYINAE Astafieva-Urbajtis, 1983

Reference: *Sovmestnaia Sovetsko-Mongolskaia Paleontologicheskaja Ekspeditsia, Trudy*, 20: 71

Type genus: †*Undulomya* Fletcher, 1946

UNDULOSTREINI Harry, 1985 [1 October]

Reference: *The Veliger*, 28(2): 146

Type genus: *Undulostrea* Harry, 1985

UNGULINIDAE Gray, 1854 [1 July]

Reference: *Annals and Magazine of Natural History*, ser. 2: 1425, 1426

Type genus: *Ungulina* Bosc, 1801

Remarks: -inae [as -ana], Bronn (1862: 475, 500); -oidea, Nevesskaja et al. (1971: 18). See also Remarks under Mysiidae.

UNICARDIIDAE P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, (11): 1099

Type genus: †*Unicardium* d'Orbigny, 1850

Remarks: See Mactromyidae and Unicardiopsidae.

UNICARDIOPSIDAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 634

Type genus: †*Unicardiopsis* Chavan, 1969

Remarks: Not available (no description) from H. A. Vokes (1967: 247), who established Unicardiopsidae as a “new name” for “Unicardiidae Fischer, auct.”. The name of the type genus is not available (no description) from Chavan in 1962.

UNIONINAE Rafinesque, 1820 [September]

Reference: *Annales Générales des Sciences Physiques* [Bruxelles], 5: 290

Type genus: *Unio* Philipsson, 1788

Remarks: Original spelling Uniodia. -idae [as Uniodae], Fleming (1822: 506); -oidea [as -oideae], Hannibal (1912: 119); -ini, Graf (2002: 66). Precedence over simultaneously published Anodontinae determined by First Reviser action by Morrison (1956: 16). Placed

on the Official List by Opinion 495 (1957: 293), but attributed in error to Fleming, 1828.

UTSCHAMIELLIDAE Kolesnikov, 1977

Reference: *Paleontologicheskii Zhurnal*, (1977)3: 45

Type genus: †*Utschamiella* Ragozin, 1937

Remarks: Attributed by Kolesnikov to Kolesnikov, 1974, but we could not trace that the name was established earlier than 1977.

VACUNELLIDAE Astafieva-Urbajtis, 1973

Reference: *Paleontologicheskii Zhurnal*, 1973(1): 18

Type genus: †*Vacunella* Waterhouse, 1965

Remarks: -ini, Waterhouse (2001: 148).

VASCONELLINAE Scarlato & Starobogatov, 1979

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 6: 23

Type genus: †*Vasconella* Boussac, 1911

VASCONIELLIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 23, 34

Type genus: *Vasconiella* Dall, 1899

VAUGONIINAE Kobayashi, 1954

Reference: *Japanese Journal of Geology and Geography, Transactions*, 25(1–2): 68

Type genus: †*Vaugonia* Crickmay, 1930

Remarks: -idae, M. R. Cooper (1991: 10).

VELESUNIONINAE Iredale, 1934 [9 May]

Reference: *The Australian Zoologist*, 8(1): 58

Type genus: *Velesunio* Iredale, 1934

VENERICARDIINAE Chavan, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 554

Type genus: *Venericardia* Lamarck, 1801

VENERIDAE Rafinesque, 1815

Reference: *Analyse de la nature*: 146

Type genus: *Venus* Linnaeus, 1758

Remarks: Original spelling Veneridia. -inae, Swainson (1840: 372); -oidea [as -acea], Gill (1871: 19) [Keen (in Moore, ed., 1969: 670) attributed superfamily rank to Menke (1830, sic!; also 1828: 69); Menke did use the spelling Veneraceae, but the context indicates family rank was meant].

VENIELLINAE Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 538

Type genus: †*Veniella* Stoliczka, 1870

Remarks: Dall (1889a: 54) had earlier used Veniliidae. He did not give explicit reasons why he introduced the name Veniellinae, but *Veniella* is a substitute name for *Venilia* S. G. Morton, 1833 (non Duponchel, 1829), and Veniellinae was probably intended to be a substitute name for Veniliidae. -idae [declared new], R. N. Gardner (2005: 359).

VENILIIDAE Meek, 1864 [April]

Reference: *Smithsonian Miscellaneous Collections*, 7(177): 13, 33

Type genus: †*Venilia* S. G. Morton, 1833

Remarks: Invalid: Type genus a junior homonym of *Venilia* Duponchel, 1829 [Lepidoptera]; see Veniellinae.

VEPRICARDIINI Kafanov & Starobogatov, 1977

Reference: [in Kafanov & Popov] *Paleontologicheskii Zhurnal*, 1977(3): 62

Type genus: *Vepricardium* Iredale, 1929

VERTICORDIIDAE Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b

Type genus: *Verticordia* J. de C. Sowerby, 1844

Remarks: -oidea, Scarlato & Starobogatov (1979a: 24).

VESICOMYIDAE Dall & Simpson, 1901 [November]

Reference: *United States Fish Commission Bulletin*, 20(1): 496

Type genus: *Vesicomya* Dall, 1886

Remarks: Original spelling Vesicomycidae.

VETERANELLINAE Chen, Liu & Lan, 1983 [November]

Reference: *Acta Paleontologica Sinica*, 22(6): 618 [Chinese text], 626 [English text]

Type genus: †*Veteranella* Patte, 1926

VLASTIDAE Neumayr, 1891

Reference: *Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, 58: 724

Type genus: †*Vlasta* Barrande, 1881

Remarks: Original spelling “Vlastiden” (vernacular). First latinized by Grobben (1892a: 142; 1892b: 373). -inae, Newell & LaRocque (in Moore, ed., 1969: 247).

VOLINAE Teppner, 1922 [30 December]

Reference: *Fossilium Catalogus*, I, Pars 15: 221

Type genus: *Vola* Mörch, 1853

Remarks: Original spelling Volainae.

VOLVICERAMINAE Heinz, 1932

Reference: *Mitteilungen aus dem Mineralogisch-Geologischen Staatsinstitut in Hamburg*, 13: 22

Type genus: †*Volviceramus* Stoliczka, 1871

Remarks: Name only, no description. Not available, unless discovery of an author who used the name as valid before 2000.

VULSELLIDAE Gray 1854 [1 July]

Reference: *Annals and Magazine of Natural History*, ser. 2: 1427

Type genus: *Vulsella* Röding, 1798

Remarks: -inae [as -ana], Bronn (1862: 474, 498).

WALLOWACONCHIDAE Yancey & Stanley, 1999 [February]

Reference: *Palaeontology*, 42(1): 5

Type genus: †*Wallowaconcha* Yancey & Stanley, 1999

WANWANIIDAE Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 10

Type genus: †*Wanwania* Kobayashi, 1933

Remarks: Established as a family of bivalves, but now classified in the separate class Rostroconchia.

WEYLINAE Kasum-Zade, 2003

Reference: [Advance in research of Mesozoic bivalve mollusks in Azerbaijan Order Pectinida: revision and systematics]: 58, 86

Type genus: †*Weyla* Boehm, 1922

XENOMYTILINAE Squires & Saul, 2006 [2 November]

Reference: *The Veliger*, 48(3): 126

Type genus: †*Xenomytilus* Squires & Saul, 2006

XYLOPHAGIDAE Purchon, 1941 [February]

Reference: *Journal of the Marine Biological Association of the United Kingdom*, 25: 32, 35

Type genus: *Xylophaga* Turton, 1822

Remarks: Original spelling Xylophaginidae. -inae, and spelling corrected to Xylophaginae, Turner (1955). Turner (in Moore,

ed., 1969: 721) emended the spelling to Xylophaginae to avoid homonymy with “Xylophagidae Latreille, 1807”, by Turner believed to be based on “*Xylophagus* Meuschen, 1778”. Xylophagi was used by Latreille for a family of Coleoptera, but it was not based on an included genus, and, furthermore, Meuschen (1778) has been placed on the Official Index by Opinion 260. Nevertheless, there is a family Xylophagidae Fallén, 1810, based on *Xylophagus* Meigen, 1803 [Diptera]. However, under Art. 55.3.1, a change in spelling can be done only by the Commission, and the Commission has to be petitioned to amend the spelling of the bivalve name, which is in current use at subfamily level.

YOLDIELLINAE Allen & Hannah, 1986 [November]

Reference: *Journal of Conchology*, 32(4): 235

Type genus: *Yoldiella* Verrill & Bush, 1897

Remarks: Not available (no description) from Allen (1978: 392, 396, as -idae); nor from Allen (1985: 356, as -idae).

YOLDIINAE Dall, 1908 [October]

Reference: *Bulletin of the Museum of Comparative Zoology*, 43(6): 379

Type genus: *Yoldia* Möller, 1842

Remarks: Independently declared new by Habe (1977: 25). -idae [declared new], Allen & Hannah (1986: 233).

ZACHSIINAE Habe, 1977

Reference: *Systematics of Mollusca in Japan. Bivalvia and Scaphopoda*: 301

Type genus: *Zachsia* Habe, 1952

Remarks: Genus name not available (no type species designated) from Bulatoff & Rjabtschikoff, 1933.

ZADIMERODIIDAE Guo, 1988

Reference: *Yunnan Geology*, 7(2): 119

Type genus: †*Zadimerodia* Guo, 1988

Remarks: Not available (family diagnosed, but type genus a nomen nudum) from Guo (1985: 172).

ZEALIDIDAE Scarlato & Starobogatov, 1979

Reference: *Trudy Zoologicheskogo Instituta*, 80: 19, 25

Type genus: †*Zealeda* Marwick, 1924

Remarks: -inae, Schileyko (1989: 94).

ZENATIINAE Dall, 1895 [March]

Reference: *Proceedings of the Malacological Society of London*, 1(5): 209, 212

Type genus: *Zenatia* Gray, 1853

ZIRFAEINAE Gray, 1851 [1 November]

Reference: *Annals and Magazine of Natural History*, ser. 2, 8(47): 381, 385

Type genus: *Zirfaea* Gray, 1842

Remarks: Original spellings *Zirfaeina* and *Zirfaeana*.

List of Bivalve Names Above the Family-Group

It is often abusively – and erroneously – said that the International Code of Zoological Nomenclature does not cover “higher categories” names, that is, names above the rank of superfamily. In fact, whereas there are indeed many specific articles of the Code that regulate specifically species-group, genus-group, and family-group names, Art. 1.2.2 of the Code explicitly states that “Articles 1–4, 7–10, 11.1–11.3, 14, 27, 28 and 32.5.2.6 also regulate names of taxa at ranks above the family group”. These articles cover the criteria of publication (Arts. 7–9) and some of the criteria of availability (Arts. 10, 11.1–11.3, 14). It is true, however, that some of the basic principles of the Code, such as the Principle of Priority (Art. 23) and the Principle of Typification (Art. 61), do not extend to the higher-categories names. Dubois has proposed an elaborate set of rules for the full incorporation of higher-ranked taxa into the Code (Dubois 2005a, b, 2006), but there is no unanimity in the Commission whether this is a pressing issue for the next edition of the Code. Earlier than Dubois, and of immediate relevance to the present Nomenclator, Starobogatov (1984, 1991) had proposed, and implemented, a system that recognized three categories of names (phylum-group, class-group and order-group) and essentially extended the Principle of Typification to these higher taxonomic categories. Starobogatov also proposed standard endings, for example, -iformes for order, -oidei for suborder, and -oinei for infraorder.

One rationale that has driven us in compiling the present nomenclator is the independence of the family-group names and higher category names. For instance, the family Arctidae and the suborder Arctidina, although both based on/including the genus *Arctica*, belong to two different groups of names and thus have different authors, respectively Newton, 1891, and Newell, 1965. Although an attempt has been

made in the classification that follows this list to “normalize” the names for the subclasses and orders, these names are listed in the Nomenclator with their original spellings and endings.

ACEPHALA Cuvier, 1798

Reference: *Tableau élémentaire de l'histoire naturelle des animaux*: 378, 414

Remarks: Original spelling “Acéphales” (vernacular). First latinized by Duméril (1806: 168). Established as a division of molluscs including all the bivalves, plus tunicates, brachiopods and barnacles. See also Aglossa, Cormopoda, Ginglymaconcha, Lipocephala and Tetrabanchia.

ACEPHALOPHORA Blainville, 1825

Reference: *Manuel de malacologie et de conchyliologie*: 508

Remarks: Established as a class of Malacozoa including the orders Palliobranchiata (= brachiopods), Rudista, Lamellibranchiata, and Heterobranchiata (= Ascidiacea and salps).

ACTINODONTA Dechaseaux, 1952

Reference: [in Piveteau, ed.] *Traité de paléontologie*, 2: 266

Remarks: Established as a suborder of Taxodonta including the families Lyrodesmidae, Ambonychiidae, and Anthracosiidae. Attributed by Dechaseaux to Douvillé (1912: 1679), but Douvillé merely cited the genus *Actinodonta* [Phillips, 1848]. [See also Actinodontidae in family list]. Spelling and rank emended by Newell (1965: 16) to order Actinodontoida; by Pojeta (1978: 232) to subclass Actinodontia.

ADAPEDONTA Cossmann & Peyrot, 1909

Reference: *Actes de la Société Linnéenne de Bordeaux*, 63(3): 146

Remarks: Established as a suborder containing the superfamilies Edentulacea, Myacea, Panopacea and Solenacea. Treated by Chavan (1952c: 119) as a superfamily, and not available as such (not based on a genus).

ADESMACEA P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*: 1130

Remarks: Established as a suborder of the order Tetrabanchia, containing the families Pholadiidae and Teredinidae. See also family list.

AGLOSSA Lovén, 1848

Reference: *Kongliga Vetenskaps-Academiens Handlingar*, (1848): 104 [reprint], and table between pp. 104 and 105

Remarks: One of the two divisions of molluscs, established as a substitute name for Acephala, including Lamellibranchiata and Brachiopoda.

ALASMODESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 136

Remarks: Vernacular name only. Established as a division of the bivalves including the “Anomiiden”.

AMBONODONTA Grobben, 1892

Reference: *Arbeiten aus dem Zoologischen Institut der Universität Wien und der Zoologischen Station in Triest*, 10(2): 142

Remarks: Also published in Grobben (1892b: 373). Established as a subclass, containing the orders Eutaxodonta, Heterodonta, Schizodonta, and Anisomyaria.

AMBONYCHIIDINA Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 18

Remarks: Established as a suborder, containing the superfamilies Ambonychioidea, Inoceramoidea, and Alatoconchoidea.

AMEODONTIDA Stenzel, Krause & Twining, 1957 [15 February]

Reference: *The University of Texas Publication*, 5704: 43

Remarks: Established as an order of the class Protobranchia, including the superfamilies Nuculoidea and Nuculanoidea.

AMYARIA Dall, 1884 [18 July]

Reference: *Science*, 4(76): 51

Remarks: Established conditionally as an order, containing the family Chlamidoconchidae, itself monotypic on *Chlamydoconcha orcutti* Dall, 1884. See also Chlamydoconchina.

ANADESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 150

Remarks: Vernacular name only. Established as a division of the bivalves including “Pholaden” and “Teredinen”.

ANATINACEA P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*: 1154

Remarks: Established as a suborder of the order Dibranchia containing the families

Cuspidariidae, Solenomyidae, Clavagellidae, Anatinidae, Pandoridae, Chamostreidae, Verticordiidae and Lyonsiidae. Spelling emended to Anatinina (in synonymy of Laternulina) by Scarlato & Starobogotov (1978: 223). See also Laternulacea and Pandoracea.

ANISOMYARIA Neumayr, 1884

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, Abt. 1, 88(2): 412

Remarks: Original spelling “Anisomyarier” (vernacular). Latinized by P. Fischer (1886: 921). Established as an order containing “Heteromyarier” (Aviculidae, Mytilidae, Prasinidae and Pinnidae) and “Monomyarier” (Pectinidae, Spondylidae, Anomiidae and Ostreidae). Ranked as suborder by Abbott (1954: 349); as superorder [in the synonymy of Eupteriomorphia] by Amler (1999: 239). See also Dysodonta.

ANODONTODA Haeckel, 1868

Reference: *Natürliche Schöpfungs-Geschichte*, ed. 1: 415

Remarks: Established as an alternative name for Acephala.

ANOMALOBANCHIA Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 231

Remarks: Established as an order containing the suborder Laternuliformes, Pandoriformes and Brechitiformes.

ANOMALODESMACEA Dall, 1889

Reference: *American Journal of Science*, ser. 3, 38: 452, 457, 460

Remarks: Established as an order of Pelecypoda, containing the suborders Solenomyacea, Anatinacea, Myacea, Ensiphonacea or Tubicolae, and Adesmacea. Ranked as suborder by Haas (1929: 19); as subclass by Winckworth (1932: 247); as superorder by Amler (1999: 244). Spelling emended by Keen (1963: 93) to (subclass) Anomalodesmata.

ANOMIAINA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 418

Remarks: Established at rank below suborder (Ostracea), containing the family Anomiidae only. Spelling and rank emended by Dall (1889b: 459, 460) to suborder Anomiacea.

ANTIPLEUROIDA Kříž, 2007 [November]
Reference: *Palaeontology*, 50(6): 1352, 1361
Remarks: Established as an order containing the superfamily Antipleuroidea only.

APPENDICULATA P. Fischer, 1886 [30 April]
Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*: 923
Remarks: Established simultaneously for two different subdivisions of the Pelecypoda: (1) as a division of the order Tetrabanchia including the genera *Cardium*, *Tapes* and *Dosinia*; (2) as a division of the order Dibranchia including the genera *Thracia*, *Tellina* and *Solemya*.

ARCACEA Gray, 1854 [1 May]
Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 417
Remarks: Established as a suborder containing the families Trigoniidae and Arcidae. Spelling and rank emended to order Arcacea by Stolicka (1870: 8 γ); to order Arcoida by Newell (1965: 16).

ARCHIHETERODONTA Giribet, 2007 [November]
Reference: [in Taylor et al.] *Zoologica Scripta*, 36: 601
Remarks: Attributed by Taylor et al. to “Giribet, in press”, but not published at the time of publication of their paper; treated by them as a division of the Heterodonta containing the superfamily Crassatelloidea only. Declared new by Giribet (2008: 124, 126), established as unranked division of the Heterodonta containing the superfamilies Carditoidea, Crassatelloidea, and Astartoidea.

ARCTICINA Newell, 1965
Reference: *American Museum Novitates*, 2206: 20
Remarks: Established as a suborder containing the superfamilies Arcticoidea, Dreissenoida, Glossoidea, Corbiculoidea and Veneroidea. Spelling and rank emended to infraorder Arcticoinei [declared new] by Starobogatov (1992: 22, 24).

ASCOLIÉPHORES Récluz, 1869
Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): 31, table between pp. 34 and 35
Remarks: Vernacular name only. Established as a suborder of the order “Disiphoniphores”, including the “tribes” “Cratérodimaies” (including the family Eucharidae only) and “Cratéromonaires” (including the families Cycladidae, Dreissenidae, Cardiidae, Tridacni-

dae, Lucinidae, Erycinidae, Galeommatidae, Solemyidae, Chamidae, and Rudistidae).

ASIPHONIA Rafinesque, 1815
Reference: *Analyse de la nature*: 147
Remarks: Established as a suborder of the “order” Bivalvia, containing the families Pediferia, Byssiferia and Ostreacia. Spelling emended to Asiphonida by Fleming (1828: 381) and by S. P. Woodward (1854: 252, 253), in both cases with an extension similar to that of Rafinesque. See also Asiphonidae in family list.

ASIPHONIPHORES Récluz, 1869
Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): 30, table between pp. 34 and 35
Remarks: Vernacular name only. Established as an order of the subclass Dimyaria, including the families Trigoniidae, Nuculidae, Arcidae, and Etheriidae.

ASIPHONOPHORA Gray, 1854 [1 May]
Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 415
Remarks: Established as a subclass of the class Conchifera [= bivalves] including the orders Lasiacea, Unionacea, and Pectinacea.

ASTARTEDONTA Korobkov, 1954
Reference: *Spravochnik i metodicheskoe rukovodstvo po tretichnym molliuskam*: 57, 134
Remarks: Established as a suborder of Heterodonta containing the superfamily Astartoidea. Spelling emended to Astartedontina by Cox (1960: 83, 85).

ASTARTIDA Scarlato & Starobogatov, 1971
Reference: [in Nevesskaja et al.] *Paleontologicheskii Zhurnal*, 1971(2): 16
Remarks: Established as an order including the superfamilies Astartoidea, Crassatelloidea, Hiatelloidea, Babinkoidea, Lucinoidea, Cyrenoidoidea, Kellioidea, Leptonoidea, Galeommatoidea, Chlamydoconchoidea, Pisidioidea, Cyamioidea, and Donacoidea. Ranked as suborder, spelling emended to Astartina, by Scarlato & Starobogatov (1979a: 22).

ASTHENODONTA Dall, 1895 [March]
Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 557
Remarks: A division of the order Teleodermacea containing the superfamilies Myacea and Adesmacea. Spelling and rank emended by Cox (1960: 80) to order Asthenodontida.

ATRACHIA Swainson, 1840Reference: *A treatise on malacology*: 254

Remarks: Established as a “tribe” [= suborder] containing the families Arcidae, Aviculidae, Ostreidae, Etheriidae and Unionidae.

AUTOBRANCHIA / AUTOBRANCHIATA

See Autolamellibranchiata.

AUTOLAMELLIBRANCHIATA Grobben, 1894Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, 103 (1[1]): 73

Remarks: Established as an order of the subclass Lamellibranchia containing the suborders Eutaxodonta, Heterodonta and Anisomyaria. Spelling and rank emended by Kolesnikov (1977: 44) to superorder Autobranchia; by Waller (1978: 350) to subclass; by Amler (1999: 238) to infraclass.

AVICULACEA Steinmann, 1903Reference: *Einführung in die Paläontologie*: 229, 249

Remarks: Established as a division of Anisomyaria of unspecified rank, containing the families Aviculidae, Inoceramidae, Limidae, Pectinidae, and Ostreidae. Spelling and rank emended by Iredale (1939: 319) to suborder Aviculiformes containing the families Pteridae, Reniellidae and Isognomonidae.

AVICULOPECTINOIDEI Starobogatov, 1992Reference: *Ruthenica*, 2(1): 21, 23

Remarks: Established as an infraorder of the suborder Pterioidei containing the superfamilies Posidonioidea, Aviculopectinoidea, Euchondrioidea and Buchioidea. Spelling and rank emended by Waterhouse (2001: 117) to suborder Aviculopectinidina [declared new], including the superfamilies Aviculopectinoidea, Chaenocardioidea, Pterinopectinoidea, Pseudomonotoidea and Euchondrioidea.

BIFORIPALLA Latreille, 1824Reference: *Annales des Sciences Naturelles*, 3: 332

Remarks: Established as an order containing the families “Mytilacés” and “Nayades”.

BIMUSCULOSA Reeve, 1841Reference: *Conchologia systematica*, 1: 4, 32

Remarks: Established as an order of the class Trochopoda, containing the families Tubicola, Pholadaria, Solenacea, Myaria, Mactracea, Lithophaga, Nymphacea, Conchacea, Car-

diacea, Arcacea, Trigonacea, Naiades, and Chamacea.

BIVALVIA Linnaeus, 1758Reference: *Systema Naturae*, ed. 10, 1: 645Remarks: Established as a division of Vermes Testacea containing the genera *Pholas*, *Mya*, *Solen*, *Tellina*, *Cardium*, *Donax*, *Venus*, *Spondylus*, *Chama*, *Arca*, *Ostrea*, *Anomia*, *Mytilus*, and *Pinna*. Ranked by Thiele (1926: 161) as class; by Cavalier-Smith (1998: 235) as subphylum. See also Ginglymaconcha.**BOTHRIODONTEN** Vest, 1899Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 141

Remarks: Vernacular name only. Established as a division of the bivalves including “Lassaeiden” and “Galeommiden”.

BRECHITIFORMES Iredale, 1939 [25 February]Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 231

Remarks: Established as a suborder containing the family Brechitidae.

CARDIACEA Férussac, 1822 [13 April]Reference: *Tableaux systématiques des animaux mollusques*: xxxix

Remarks: Original spelling “Les Cardiacés” (vernacular). Latinized by Menke (1828: 65). Established as an order, containing the families Camacés, Bucardes, Cyclades, Nymphacés, Vénus, Lithophages, and Mactracés. Ranked by P. Fischer (1887: 1033) as suborder containing the families Cardiidae, Tridacnidae and Lunulacardiidae. Spelling and rank emended by Naumov, Scarlato & Fediakov (1987: 246) to order Cardiiformes and suborder Cardioidei.

CARDINIACEA Moore, 1952Reference: [in Moore et al.] *Invertebrate fossils*: 411, 419Remarks: Established as a suborder of Schizodonta; family composition not given, but *Anthracomya*, *Unio* and *Amnigenia* cited as examples.**CARDIODONTA** Scarlato & Starobogatov, 1969Reference: *Soveshchanie po probleme “Puti i zakonmernosti ...”*: 9

Remarks: Established as a suborder of Gastropemta containing the superfamilies Cardioidea, Tridacnoidea, Mactroidea, Solenoidea and Tellinoidea.

CARDITACEA Dall, 1889 [December]

Reference: *The American Journal of Science*, ser. 3, 38: 460

Remarks: Established as a suborder of the order Teleodesmacea. No description, no contents given. Spelling and rank emended by Scarlato & Starobogatov (in Nevesskaja et al., 1971: 17) to order Carditida [declared new], containing the superfamilies Carditoidea, Kalenteroidea, and Condylocardioidea.

CHAMACEA Stoliczka, 1871 [1 March]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous fauna of southern India*, vol. 3, parts 5–8: 223

Remarks: Established as an order, including the families Verticordiidae, Tridacnidae, Chamidae, Chamostreidae, and Hippuritidae. Treated by Steinmann & Döderlein (1888: 257, 269) as a suborder of the order Heterodonta, including the families Chamidae, Monopleuridae, Caprinidae, and Hippuritidae.

CHELISOMIDAE Swainson, 1840

Reference: *A treatise on malacology*: 254

Remarks: Established as a “tribe” [= suborder] of bivalves, without any explicitly included taxa.

CHLAMYDOCONCHINA Scarlato & Starobogatov, 1975

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 5: 6

Remarks: Established as a suborder containing the superfamily Chlamydoconchoidea only. An absolute synonym of Amyaria Dall, 1884.

CLADOPODA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 237

Remarks: Established as an order of the class Conchophora, including the genera *Pholas*, *Teredo*, and *Aspergillum*.

CLAUSICONCHAE Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: table

Remarks: Original spelling “Clausiconques” (vernacular). Latinized by Berthold (1827: 208). Established as a division of the Tubipalla including the families Camacés, Cardiacés, Cycladines, Vénérides, Tellinides, Corbulés, and Mactracés.

CLAVAGELLINA Newell, 1965

Reference: *American Museum Novitates*, 2206: 21

Remarks: Established as a suborder containing the superfamily Clavagelloidea. Used at same rank and independently declared new by Scarlato & Starobogatov (1969: 9).

COLLOCONCHIDA Cox, 1960

Reference: *Proceedings of the Malacological Society of London*, 34(2): 85

Remarks: Established as an order of the subclass Pteriomorphia containing the superfamily Ostreacea. Ranked by Habe (1977: 106) as suborder (in the synonymy of Ostreina).

CONCHACEA P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*: 1068

Remarks: Established as a suborder including the families Megalodontidae, Cyprinidae, Pachydomidae, Veneridae, Petricolidae, Glaucomyidae, Cyrenidae, Rangiidae, Cyrenellidae, Ungulinidae, Unicardiidae, Tancrediidae, Donacidae, Psammobiidae, and Solenidae.

CONCHAE J. Férussac, 1801

Reference: *Mémoires de la Société Médicale d'Emulation*, 4: 381, 388, 398

Remarks: Established as a division of the class “Musculites” including the freshwater bivalves. See also family-group names.

CONCHIFERA Lamarck, 1818 [July]

Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 411

Remarks: Established as a class, including the orders “Conchifères dimyaires” and “Conchifères monomyaires”. See also Cormopoda and Ginglymaconcha.

CONCHOPHORA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 236

Remarks: Established as a class, including the orders Cladopoda, Pachypoda, Leptopoda, Phyllopoda, Pogonopoda, and Micropoda.

CONOCARDIIDA Newell, 1965

Reference: *American Museum Novitates*, 2206: 17

Remarks: Established as an order of bivalves, containing the superfamily Conocardioida only. Name attributed by Newell to Neumayr (1891: 740) who, however, used “Conocardiiden” (vernacular) as a family. Spelling and rank emended by Starobogatov (1977: 134) to order Conocardiida and suborder Conocardiina; by Scarlato & Starobogatov

(1979a: 24) to superorder Conocardioida (in synonymy of Septibranchia). Now classified in the class Rostroconchia.

CORMOPODA Burmeister, 1837

Reference: *Handbuch der Naturgeschichte*, 2: iv, 478

Remarks: Established at the rank of order, as a substitute name for Acephala, Pelecypoda, Conchifera and Lamellibranchia.

CRASPEDODESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 136

Remarks: Vernacular name only. Established as a division of the bivalves including the "Dimyarier" families "Mytiliden" and "Dreisseniden" and the "Monomyarier" family "Prasiniden".

CRASSIPEDA Lamarck, 1818

Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 422, 425, 426

Remarks: Original spelling "Crassipèdes" (vernacular), established as a division (pp. 426) or section (p. 425) of the "Dimyaires", including "les Tubicolées, les Pholadaires, les Solénacées, les Myaires". Latinized by Children (1822: 79, as Crassipeda; same composition as Lamarck's) and Burmeister (1837: v, 488, as Crassipedia) as a division of the Dimyia, including the families Myidae and Solenidae.

CRATÉRODIMAIRES Récluz, 1869

Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): 30, table between pp. 34 and 35

Remarks: Vernacular name only. Used at the rank of "tribe" (below suborder, above family) at three occasions in the classification of the Dimyaria; see "Scoliéphores", "Ascoliéphores", and "Monosiphoniphores".

CRATÉROMONAIRES Récluz, 1869

Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): 30, table between pp. 34 and 35

Remarks: Vernacular name only. Used as a "tribe" (below suborder, above family) at three occasions in the classification of the Dimyaria; see "Scoliéphores", "Ascoliéphores", and "Monosiphoniphores".

CRYPTODESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 146

Remarks: Vernacular name only. Established as a division of the bivalves including the "Solemyiden".

CRYPTODONTA Neumayr, 1884

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, Abt. 1, 88(2): 411

Remarks: Original spelling "Cryptodonten" (vernacular). Latinised by P. Fischer (1886: 921). Established as an order; ranked by Newell (1965: 16, 17) as subclass containing the orders Solemyoida, Praecardioida, and ?Conocardioida. Spelling emended by Scarlato & Starobogatov (1969: 8) to (order) Cryptodontida. See also Palaeoconchae.

CTENIDIOBRANCHIA Salvini-Plawen, 1980 [14 April]

Reference: *Malacologia*, 19(2): 264

Remarks: Established as superorder of subclass Pelecypoda, equivalent to Palaeotaxodonta, and containing the order Nuculida only.

CTENODONTA Dechaseaux, 1952

Reference: [in Piveteau, ed.] *Traité de paléontologie*, 2: 261, 262, 271

Remarks: Established as a suborder including the families Ctenodontidae, Nuculidae, Lediidae, Solemyidae, Praecardiidae, Grammysiidae, Antipleuridae, Vlastidae, and Solenopsidae. Attributed by Dechaseaux to Douvillé (1912: 1679, 1681) who however merely cited the genus *Ctenodonta*.

CUSPIDARIIDA Starobogatov, 1970

Reference: *Fauna molliuskov i zoogeograficheskoe raionirovanie kontinental'nykh vodoemov zemnogo shara*: 89

Remarks: Established as an order containing the superfamily Cuspidarioidea only. Attributed by Starobogatov to Dall, 1886 [see family list]. Declared new order by Scarlato & Starobogatov (in Nevesskaja et al., 1971: 19). Spelling and rank emended by Scarlato & Starobogatov (1983: 12) to order Cuspidariiformes and suborder Cuspidarioidei.

CYCLODONTA Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Philadelphia*, 3(3): 548

Remarks: Established as a division of the order Teleodesmacea containing the superfamilies Cardiacea, Tridacnacea and Isocardiacea. Spelling and rank emended by Keen (1963: 91) to suborder Cyclodontina containing the superfamily Cardiacea.

CYPRICARDIACEA Moore, 1952

Reference: [in Moore et al.] *Invertebrate fossils*: 411, 439

Remarks: Established as a suborder of Heterodonta; family composition not given, but *Cypricardella*, *Cypricardinia*, *Arctica* and *Veniella* cited as examples.

CYRENACEA Moore, 1952

Reference: [in Moore et al.] *Invertebrate fossils*: 411, 440

Remarks: Established as a suborder of Heterodonta; family composition not given, but *Cyrena*, *Mercenaria*, *Dosinia*, *Cyprimeria*, and *Venericardia* cited as examples. Spelling and rank emended by Korobkov (1954: 57, 141) to suborder Cyrenodonta; by Stenzel, Krause & Twining (1957: 133) to (suborder) Cyrenina, including the superfamily Veneroidea only; by Sobetski (1977: 18) to order Cyrenoida [attributed to Nevesskaja & Eberzin, 1969; no reference given, not traceable], containing the superfamily Arcticoidea only.

CYRTODONTIDA Scarlato & Starobogatov, 1971

Reference: [in Nevesskaja et al.] *Paleontologicheskii Zhurnal*, 1971(2): 14

Remarks: Established as an order containing the suborders Arcina, Ostreina and Pteriina. Spelling and rank emended by Scarlato & Starobogatov (1979a: 21) to suborder Cyrtodontina. Independently declared new order by Cope (1996: 1010), containing the superfamilies Cyrtodontoidea and Falcato-dontoidea.

DALLICORDIOIDEI Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 12

Remarks: Established as a suborder containing the family Dallicordiidae only.

DESMODONTA Neumayr, 1884

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, Abt. 1, 88(2): 411

Remarks: Original spelling "Desmodonten" (vernacular). Latinized by P. Fischer (1886: 921). Established as an order containing the families Pholadomyidae, Corbulidae, Myidae, Anatinidae, Mactridae, Paphiidae, Glycymeridae and ?Solenidae. Ranked by Haas (1929: 18) as suborder. Spelling emended by Scarlato & Starobogatov (1969: 8) to (order) Desmodontida.

DEXTRODONTA Pchelintsev, 1959

Reference: *Geologicheskii Muzei Karpinskogo, Seriya Monograficheskaya*, 3: 36

Remarks: Established as a suborder containing the families Plesiodiceratidae, Epidiceratidae, Heterodiceratidae, Requiiniidae and Diceratidae. Treated by Eberzin (1960: 153) as a superfamily and not available as such (not based on a genus).

DIADESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 137

Remarks: Vernacular name only. Established as a division of the bivalves including the "Limiden" and "Pectiniden".

DIAPEDASTROPHIA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 238

Remarks: A division of the class Conchophora including the genera *Mya*, *Corbula*, *Mactra*, and *Nucula*.

DIBRANCHIA P. Fischer, 1886 [30 April]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*: 923; 1140 [1887]

Remarks: Established as a division of Pelecypoda, at the rank of order, containing the suborders Lucinacea, Tellinacea, and Anatinacea.

DICERATINA Yanin, 1989

Reference: *Iurskie i melovye rudisty*: 155

Remarks: Established as a suborder containing the superfamilies Diceratoidea and Epidiceratoidea. Declared again nov., and diagnosed, by Yanin (1990: 64). Spelling emended by Mainelli (1992: 264) to Diceratodonta (declared new suborder), containing the family Diceratidae only.

DIMYACEA Ridewood, 1903 [31 January]

Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 185, 193

Remarks: Established as a suborder containing the family Dimyidae. Spelling emended by Iredale (1939: 391) to suborder Dimyiformes.

DIMYARIA Lamarck, 1812

Reference: *Extrait du cours de zoologie du Muséum d'Histoire naturelle*: 105

Remarks: Original spelling "dimyaires" (vernacular), including the families Camacées, Naya-des, Arcacées, Cardiacées, Conques, Mactracées, Myaires, Solenacées, Lithophages, and

Pholadaires. Latinized by Menke (1828: 60) as suborder Dimya; by Swainson (1835: 27) as (unranked) Dimiaria; by Herrmannsen (1847: 389) as order Dimyaria.

DIODONTEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 142

Remarks: Vernacular name only. Established as a division of the bivalves including the “Dipodonten”, “Lucinen”, “Cardien”, “Limnocardien”, “Tellinen”, and “Cycladen”.

DIAGENODONTA Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Philadelphia*, 3(3): 538

Remarks: A division of the order Teleodesmacea containing the superfamilies Cypricardiacea, Astartacea, Cyrenacea, Carditacea, Chamaacea, Rudistae, Lucinacea and Leptonacea. Spelling and rank emended by Keen (1963: 91) to suborder Diagenodontida containing the superfamilies Astartacea, Carditacea, Glosacea, Arctiacea, Leptonacea, Cyamiacea and Lucinacea.

DIPLACOPHORA Horný, 1960

Reference: *Vestník Ustredniho Ustavu Geologického*, 35(6): 479

Remarks: Established as an order containing the family Babinkidae only.

DIPLOPHONIA Rafinesque, 1815

Reference: *Analyse de la nature*: 146

Remarks: Established as a suborder of the order Bivalvia, containing the families Hypogidia and Veneridia.

DISIPHONIPHORES Récluz, 1869

Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): 29, 30, table between pp. 34 and 35

Remarks: Vernacular name only. Established as an order of the subclass Dimyaria, including the suborders “Scoliéphores” and “Ascoliéphores”.

DITHYRA Turton, 1822

Reference: *Conchylia insularum britannicarum*: vii, ix

Remarks: Established as an order and equivalent to bivalves.

DONACOINEI Starobogatov, 1992

Reference: *Ruthenica*, 2(1): 22, 24

Remarks: Established as an infraorder including the families Sowerbyidae, Tancrediidae and Donacidae.

DREISSENSIACEA Moore, 1952

Reference: [in Moore et al.] *Invertebrate fossils*: 411, 434

Remarks: Established as a suborder of Dysodonta; family composition not given, but *Dreissensia* [sic, = *Dreissena*] cited as example.

DREPANODONTEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 144

Remarks: Vernacular name only. Established as a division of the bivalves including the “Soleniden” and “Phariden”.

DYSODONTA Neumayr, 1884

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, Abt. 1, 88(2): 412

Remarks: Original spelling “Dysodonten” (vernacular). Latinized by Steinmann & Döderlein (1888: 279). Established as an order in synonymy of “Anisomyarier”.

ELATOBANCHIATA Menke, 1828

Reference: *Synopsis methodica molluscorum*: 57

Remarks: Established at the rank of class, as a substitute name for “Lamellibranches”. Spelling emended by Menke (1830: 97) to Elatobanchia. Rank emended by Haeckel (1896: 512) to order. See also Elatocephala and Exocardines.

ELATOCEPHALA Bronn, 1862

Reference: *Die Klassen und Ordnungen der Weichthiere (Malacozoa)*, 3(1): 18, 317

Remarks: Established as a substitute name for Elatobanchia. Elatocephala (p. 317) is an alternative original spelling.

ELEUTHERORHABDA Ridewood, 1903 [31 January]

Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 185

Remarks: Established as an order containing the suborders Dimyacea, Mytilacea and Pectinacea.

EMARGINATO-PALLIATA Bronn, 1849

Reference: *Index palaeontologicus*, Abt. 2, B, *Enumerator palaeontologicus*: 319

Remarks: Established as a division of Homomya containing the families Protocardiididae, Veneridae, Tellinidae, Petricolididae, Mactridae, Anatinidae, Myidae, Glycymeridae, Solenidae, and Pholadidae.

ENDOCARDINES Bronn, 1862

Reference: *Die Klassen und Ordnungen der Weichthiere*, 3(2): 473

Remarks: Established as an order including the family Hippuritidae only.

ENDOCÉPHALES Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: table between pp. 334 and 335

Remarks: Vernacular name only. Established as a subdivision of “Mollusques Phanérogames” including the classes “Brachiopodes” and “Conchifères” [= “Acéphales”].

ENSIPHONACEA Dall, 1889 [December]

Reference: *The American Journal of Science*, ser. 3, 38: 457, 460

Remarks: Established as a suborder of Anomalodesmacea, contents not given. See also family list.

EOPTERIOIDEI Scarlato & Starobogatov, 1983

Reference: *Vsesoiuznoe soveshchanie po izucheniiu molliuskov*, 7: 10

Remarks: Established as a suborder of bivalves, but now classified in the separate class Rostroconchia.

ERYCINACEA P. Fischer, 1887 [15 June]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*, 11: 1024

Remarks: Suborder of the order Tetrabranchia, including the families Erycinidae and Galeomatidae.

ETHERIPECTINIDINA Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 134

Remarks: Established as a suborder, containing the superfamilies Etheripectinoidea, Oxytomoidea, Aulacomyelloidea, and Pseudomonoidea.

EUDESMODONTIDA Cox, 1960

Reference: *Proceedings of the Malacological Society of London*, 34(2): 85

Remarks: Established as order of Heteroconchia containing the superfamilies Allorismatoidea, Laternuloidea, Clavagelloidea and Pholadoidea.

EUHETERODONTA Giribet & Distel, 2003

Reference: [in Lydeard & Lindberg, eds.] *Molecular systematics and phylogeography of mollusks*: 71

Remarks: Clade established at the rank of order, including all the bivalves from the Thyasiridae-Fimbriidae-Lucinidae clade, “up to” the Teredinidae-Xylophagidae clade.

EULAMELLIBRANCHIATA Pelseneer, 1889 [April]

Reference: *Bulletin Scientifique de la France et de la Belgique*, 20: 50–52

Remarks: Original spelling “Eulamellibranchiés” (vernacular); latinized, at the rank of order, by Cooke (in Harmer & Shipley, eds., 1895: 451). Established as a division of Pelecypoda, including Submytilacea, Conchacea, Myacea, Pholadacea, Clavagellidae, and Anatinacea. Spelling emended by Hescheler (1900: 65) to Eulamellibranchia.

EUPROTOBRANCHIA Nevesskaja, 2009

Reference: *Paleontologicheskii Zhurnal*, 2009(1): 6

Remarks: Established as a superorder comprising all Cambrian bivalve taxa, including the orders Fordillida and Tuarangiida.

EUPTERIOMORPHIA Boss, 1982

Reference: *Synopsis and classification of living organisms*, 1: 1113; 2: 1095

Remarks: Established as a superorder containing the orders Pterioidea, Limoida and Ostreoida.

EUTAXODONTA Grobben, 1892

Reference: *Arbeiten aus dem Zoologischen Institute der Universität Wien und der Zoologischen Station in Triest*, 10(2): 142

Remarks: Also published in Grobben (1892b: 373). Established as an order, containing the family Arcidae. Spelling emended by Cox (1960: 85) to Eutaxodontida; contents emended by Newell (1965: 7) to include the superfamilies Cyrtodontoidea and Arcoidea.

EXOCARDINES Bronn, 1862

Reference: *Die Klassen und Ordnungen der Weichthiere*, 3(2): 473

Remarks: Established as an order, as a substitute name for “Elatobranchia s. str.”, containing all the bivalves except the rudists.

EXOGRINA A. Ivanov, 1995

Reference: *Paleontologicheskii Zhurnal*, 1995(3): 28

Remarks: Established as a suborder containing the superfamilies Exogyroidea, Pycnodontoidea and Hyotissoidea.

FILIBRANCHIATA Pelseneer, 1889 [April]

Reference: *Bulletin Scientifique de la France et de la Belgique*, 20: 50–52

Remarks: Original spelling “Filibranchiés” (vernacular); latinized by Cooke (in Harmer & Shipley, eds., 1895: 448). Established as a division of Pelecypoda, including Arcidae and Trigoniidae; ranked by Cooke as an order; spelling

and rank emended by Perrier (1897: 2118) to suborder Filibranchia; by Scarlato & Starobogatov (1969: 8) to (order) Filibranchida.

FOLIOBRANCHIA Ménégaux, 1889

Reference: *Bulletin de la Société Philomatique de Paris*, ser. 8, 1: 142

Remarks: Original spelling "Foliobranches" (vernacular). Latinized by Perrier (1897: 2117). Established as an order including the families Nuculidae and Solemyidae; rank emended by Perrier to suborder. Spelling emended by Dall (1909: 100) to Foliobranchiata.

FORDILLOIDA Pojeta, 1975 [14 June]

Reference: *Bulletins of American Paleontology*, 67(287): 366

Remarks: Established as an order containing the family Fordillidae only. Spelling and rank emended by Scarlato & Starobogatov (1983: 9) to suborder Fordilloidei.

GASTROCHAENOIDEA Morretes, 1949

Reference: *Arquivos do Museu Paranaense*, 7: 48

Remarks: Established as a suborder containing the superfamily Gastrochaenoidea only. Spelling emended by Scarlato & Starobogatov (1969: 9) to Gastrochaenina [declared new].

GASTRODEUTEIA Purchon, 1958 [December]

Reference: *Centenary and Bicentenary Congress, Singapore [Dec. 2–9, 1958], Abstracts of papers*: 12

Remarks: Established at the rank of order, as a substitute name for Septibranchia.

GASTROPEMPTA Purchon, 1959 [November]

Reference: *Proceedings of the Malacological Society of London*, 33(5): 226

Remarks: Established as a suborder, containing most Eulamellibranchia. Not available (nomen nudum) from Purchon (1958: 12).

GASTROPROTEIA Purchon, 1958 [December]

Reference: *Centenary and Bicentenary Congress, Singapore [Dec. 2–9, 1958], Abstracts of papers*: 12

Remarks: Established at the rank of order, as a substitute name for Protobranchia.

GASTROTETARTIKA Purchon, 1959 [November]

Reference: *Proceedings of the Malacological Society of London*, 33(5): 226

Remarks: Established as a suborder, containing part of the Filibranchia and many Eulamellibranchia. Not available (nomen nudum) from Purchon (1958: 12).

GASTROTRITEIA Purchon, 1959 [November]

Reference: *Proceedings of the Malacological Society of London*, 33(5): 226

Remarks: Established as a suborder, containing "most Filibranchia". Not available (nomen nudum) from Purchon (1958: 12).

GINGLYMACONCHA Leach, 1852

Reference: *A synopsis of the Mollusca of Great Britain*: 244

Remarks: Established at the rank of class, as a substitute name for Bivalvia, Acephala or Conchifera.

GONIOPODA Gray, 1840 [16 October]

Reference: *Synopsis of the contents of the British Museum*, ed. 42: 137 [as Gonopoda], 150

Remarks: Established as an order containing the families Chamidae, Etheriidae, Cardiidae, Crassinidae, Crassatellidae, Isocardiidae, Lucinidae, Unionidae, Iridinidae, Mycetopodidae, Trigoniidae, and Arcidae. Gonopoda is an alternative original spelling (p. 137).

GRYPHAEINA Sobetski, 1982

Reference: [in Sobetski et al.] *Trudy Paleontologicheskogo Instituta*, 187: 127

Remarks: Established as a suborder containing the superfamilies Gryphaeoidea, Hyotissoidea, Exogyroidea and Ostreoidea.

HEMIBRANCHIA Perrier, 1897

Reference: *Traité de zoologie*, 4: 2121

Remarks: Established as an order containing the Septibranchia, Anatinacea and Tellinacea.

HEMIDAPEDONTA Cossmann & Peyrot, 1909

Reference: *Actes de la Société Linnéenne de Bordeaux*, 63(4): 282

Remarks: Established as a suborder containing the superfamilies Tellinoidea and Eunympoidea.

HETEROCONCHAE Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 414

Remarks: Established as a suborder of the order Pholadacea containing the families Myidae, Corbulidae and Pandoridae. Spelling and rank emended by Hertwig (1895: 323, 324; 1903) to order "Heteroconchen"/Heteroconchae (1895, vernacular; 1903, latinized) containing the suborders Integripalliata (Tridacnidae, Cardiidae, Cycladidae, Chamidae, rudists) and Sinupalliata (Veneridae, Tellinidae, Myidae, Solenidae, Pholadidae, Gastrochaenidae); by Cox (1960: 85) to subclass Heteroconchia, containing the orders Pantodontida and Eudesmodontida.

HETERODONTA Neumayr, 1884

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, Abt. 1, 88(2): 412

Remarks: Original spelling “Heterodonten” (vernacular). Latinised by P. Fischer (1886: 921). Established as an order containing the families “Najaden, Cardiniden, Astartiden, Crassatelliden, Megalodontiden, Chamiden (Rudisten) (Tridacnen), Eryciniden, Luciniden, Cardiiden, Cyreniden, Cypriniden, Veneriden, Gnathodontiden, Telliniden, Donaciden”. Ranked by Haas (1929: 16) as suborder; by Newell (1965: 16, 19) as subclass; by Amler (1999: 242) as superorder.

HETEROMYA Bronn, 1849

Reference: *Index Palaeontologicus*, Abt. 2, B: 263

Remarks: A division of Dimya containing the families Aviculidae, Mytilidae and Tridacnidae. Spelling emended by Philippi (1853: 361) to Heteromyaria.

HIANTICONCHAE Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: table

Remarks: Original spelling “Hianticonques” (vernacular). Latinized by Berthold (1827: 212). Taxon containing the families “Myaires, Solenidés, Pholadaires”.

HIPPURITOIDA Newell, 1965

Reference: *American Museum Novitates*, 2206: 19

Remarks: Established as an order of Heterodonta, containing the superfamilies Chamoidea, Megalodontoidea and Hippuritoidea. Spelling and rank emended by Yanin (1990: 65) to suborder Hippuritina.

HOMOEODONTA Cossmann, 1901

Reference: *Revue Critique de Paléozoologie*, 5(1): 58

Remarks: Introduced as a replacement name for (suborder) Isodonta Dall, 1900, by Cossmann erroneously treated as a junior homonym of the genus-group name *Isodonta* Buvignier, 1851.

HOMOMYA Bronn, 1849

Reference: *Index Palaeontologicus*, Abt. 2, B: 276

Remarks: A division of Dimya containing Integripalliata [see that name] and Emargino-palliata [see that name]. Spelling emended by Zittel (1881: 17, 46) to Homomyaria, a division of the order Asiphonida containing the families

Arcidae, Nuculidae, Trigoniidae, Aetheriidae, Nayadidae, and Cardiniidae.

HYRIOINA Hoeh, Bogan, Heard & Chapman, 2009

Reference: *Malacologia*, 51(2): 308

Remarks: Established as a suborder of the order Unionoida containing the family Hyriidae only.

INAPPENDICULATA P. Fischer, 1886 [30 April]

Reference: *Manuel de conchyliologie et de paléontologie conchyliologique*: 923

Remarks: Established simultaneously for two different subdivisions of the Pelecypoda: (1) as a division of the order Tetrabranchia including the genera *Ostrea*, *Mytilus*, and *Arca*; (2) as a division of the order Dibranchia including the genera *Lucina* and *Corbis*.

INCLUSAE Menke, 1828

Reference: *Synopsis methodica molluscorum*: 72

Remarks: Latinization of “Les Enfermés” of Cuvier. Established as an order of Elatobranchiata, including the families Myidae, Solenidae, Pholadidae and Tubicolae.

INTEGRIPALLIATA d'Orbigny, 1844

Reference: *Paléontologie française. Terrains crétacés*, 3: 14, 15

Remarks: Original spelling “Intégropaléales” (vernacular), containing the families Cardidae, Tridacnidae, Astartidae, Cyprinidae, Cycladidae, Lucinidae, Unionidae, Trigoniidae, Nuculidae, Arcidae, and Mytilidae. Latinised by Bronn (1849: 237, 263, 276) who used the name for three different groups of bivalves: (a) as a substitute name for Monomya, containing the families Ostreidae and Pectinidae; (b) as a substitute name for Heteromya, containing the families Aviculidae, Mytilidae, and Tridacnidae; (c) as a division of Homomya, containing the families Arcidae, Myophoriidae, Chamidae, Etheriidae, “Najades”, Carditidae, Cardidae, Cycladidae, Lucinidae, and Crassatellidae. Used by Zittel (1881: 17, 63) for a division of the order Siphonida containing the families Solemyidae, Astartidae, Crassatellidae, Megalodontidae, Chamidae, Rudistidae, Tridacnidae, Verticordiidae, Galeommatidae, Erycinidae, Lucinidae, Cardidae, Cyrenidae, and Cyprinidae.

ISOCARDIACEA Dall, 1889 [December]

Reference: *The American Journal of Science*, ser. 3, 38: 460

Remarks: Established as a suborder; name only, no description. Contents not given.

ISODONTA Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(3): 524

Remarks: Established as a division of the order Prionodesmacea containing the superfamilies Pectinoidea and Anomioidea. Name later attributed by Dall (1900) to Fischer (1886: 936), who merely cited the genus *Isodonta* Buvignier, 1851. Ranked by Moore (in Moore et al., 1952: 411) as order. Spelling emended by Scarlato & Starobogatov (1969: 8) to (order) Isodontida. See also Homoeodonta.

ISOFILIBRANCHIA Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–1929. Scientific Reports*, 5(6): 409

Remarks: Established as an order including the families Mytilidae, Dreissenidae and Musculidae. Spelling emended by Cox (1960: 85) to Isofilibranchida. Ranked by Pojeta (1978: 239) as a subclass.

ISOMYA Lankester, 1883

Reference: *Encyclopaedia Britannica*, ed. 9, 16: 711

Remarks: Established as an order of bivalves containing the suborders Integripallia (itself containing the families Arcidae, Trigoniidae, Unionidae, Lucinidae and Cyprinidae) and Sinupallia (itself containing the families Veneridae, Myidae and Pholadidae).

ISOMYARIA Steinmann, 1903

Reference: *Einführung in die Paläontologie*: 229

Remarks: A division of bivalves containing Desmodonta, Taxodonta and Heterodonta.

LAMELLIBRANCHIATA Blainville, 1816

Reference: *Bulletin des Sciences par la Société Philomatique de Paris, Zoologie*, (1816): 122

Remarks: Original spelling "Lamellibranches". Latinized by Blainville (1825: 518). Established at the rank of order, including the bivalves. See also Elatobranchiata and Cormopoda.

LAMELLIPEDIA Lamarck, 1818

Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 423, 425

Remarks: Original spelling "Lamellipèdes" (vernacular), established as a division (pp. 423) or section (p. 425) of the "Dimyaires", including "les Conques, les Cardiacées, les Arcacées, les Nayades". First latinized by Burmeister (1837: v, 483) as a division of the Dimyia, including the families Chamidae, Aviculidae, Mytilidae, "Najades", Arcidae, Cardiidae, and "Conchina".

LAMELLOTACEA Horvath, 1966

Reference: *Földtani Közlöny*, 96(1): 106 [Hungarian text], 110 [German text]

Remarks: Established as a suborder including the family Lamellotidae only.

LASIACEA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 415

Remarks: Established as an order, including the families Solemyidae and Lasaeidae.

LATERNULACEA Winckworth, 1932 [June]

Reference: *The Journal of Conchology*, 19(7): 247

Remarks: Established as an order, including the families Periplomatidae, Thraciidae, Lyonsiidae, and Pandoridae. Spelling and rank emended by Iredale (1939: 231) to suborder Laternuliformes; spelling emended by Scarlato & Starobogatov (1978: 223) to (suborder) Laternulina, and treated as a substitute name for Anatinina.

LEPIDOLEPIDES Gistel, 1848

Reference: *Naturgeschichte des Thierreichs für höhere Schulen*: 173

Remarks: Established as a division of Pelecypoda including the genera *Pectunculus*, *Arca*, *Pinna*, and *Avicula*.

LEPTODESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 149

Remarks: Vernacular name only. Established as a division of the bivalves including the "Gastrochaenen", "Clavagellen", and "Brechiten".

LEPTONACEA Dall, 1889 [December]

Reference: *The American Journal of Science*, ser. 3, 38: 459, 460

Remarks: Established as a suborder of Telodesmacea. Spelling emended by Scarlato & Starobogatov (1979a: 22) to (suborder) Leptonina [declared new].

LEPTOPODA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 237

Remarks: Order of the class Conchophora including the genera *Macra* and *Nucula*.

LIMACEA Moore, 1952

Reference: [in Moore et al.] *Invertebrate fossils*: 411, 432

Remarks: Established as a suborder of Dysodonta; family composition not given, but *Lima*

cited as example. Spelling and rank emended by Waller (1978: 351) to order Limoida; by Carter, Campbell & Campbell (2000: 63) to suborder Limina; by Kasum-Zade (2003: 59, 86) to suborder Limoina; by Waterhouse (2008: 129) to suborder Limidina.

LIPOCEPHALA Lankester, 1883

Reference: *Encyclopaedia Britannica*, ed. 9, 16: 633, 648, 684

Remarks: Established above the rank of class, as one of the two branches of the phylum Mollusca, as a substitute name for Acephala, including the class Lamellibranchia only.

LIPODONTA Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 229

Remarks: Established at the rank of order as a substitute name for Palaeobranhia. Spelling emended by Cox (1960: 85) to Lipodontida. Ranked as suborder by Keen (1963: 90); as subclass by Cope (1995: 364).

LITHIOTINA Benini & Loriga, 1977 [September]

Reference: *Bollettino della Società Paleontologica Italiana*, 16(1): 37

Remarks: Established as a suborder of Pterioidea including the superfamily Lithiotoidea only.

LOBOCONCHA Salvini-Plawen, 1985

Reference: [in Trueman & Clarke, eds.] *The Mollusca*, vol. 10: 136

Remarks: Clade including the Scaphopoda and the Bivalvia.

LUCINACEA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 415

Remarks: Established as a suborder of the order Unionacea including the family Lucinidae only. Spelling and/or rank emended by H. Adams & A. Adams (1857: 466) to order, including the families Lucinidae, Ungulinidae, Laseidae, Leptonidae, Galeommidae, Solemyidae, Astartidae, Unionidae, Mutelidae, Aetheriidae, Mytilidae, Modiolarciidae, Dreissenidae, Vulsellidae, and Aviculidae; by Korobkov (1954: 81) to suborder Lucinodonta, including the superfamilies Lucinacea, Erycinacea, Tellinacea, Solenacea, Mactracea, Chamacea, and Cardiacaea; by Stenzel, Krause & Twining (1957: 101) to suborder Lucinina; by Sobetski (1977: 18) to order Lucinoida; by Pojeta (1978: 230, 242) to subclass Lucinata; by Liljedahl (1992: 206) to order Lucinida and subclass Lucinoida.

LYRODESMATINA Scarlato & Starobogatov, 1971
Reference: [in Nevesskaja et al.] *Paleontologicheskii Zhurnal*, (1971)2: 13

Remarks: Established as a suborder including the superfamilies Lyrodesmatoidea, Palae-anodontoidea and Nyassoidea.

MACROCILIOBRANCHIA Atkins, 1938 [May]

Reference: *Quarterly Journal of Microscopical Science*, new. ser., 80: 425, 430

Remarks: Established as a division of Lamellibranchia, including Protobranchia, Filibranchia, Eulamellibranchia, and Septibranchia.

MACRODESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 138

Remarks: Vernacular name only. Established as a division of the bivalves including the “Pinniden”.

MACROTRACHIA Swainson, 1840

Reference: *A treatise on malacology*: 254, 256

Remarks: Established as a “tribe” [= suborder] of bivalves including the families Tellinidae, Myidae, Pholadidae, Saxicavidae and Chamiidae.

MACTRACEA Dall, 1889 [December]

Reference: *The American Journal of Science*, ser. 3, 38: 460

Remarks: Established as a suborder of the order Teleodesmacea. Contents not given.

MALLEACEA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 417

Remarks: Established as a suborder of the order Pectinacea, containing the family Pteridae only.

MEGALODONTOIDEI Starobogatov, 1992

Reference: *Ruthenica*, 2(1): 21, 23

Remarks: Established as a suborder of Hippuritiformes including the families Plethocardiidae, Tusayanidae, Megalodontidae, Pachyrismatidae, ?Ferraziidae, and ?Pterocardiidae.

MESOMYONA Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: 331 and table

Remarks: Original spelling “Mésomyones” (vernacular). Latinized by Berthold (1827: 202). Established as a division of the class “Conchifères”, including the families Ostracés, Pectinides, and Oxygones.

MESOSYNTHETA Purchon, 1987

Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 316(1177): 283, 286, 292

Remarks: Established as an order including the suborders Trigonioidea and Unionioidea, the latter including the superfamilies Unionacea, Crassatellacea, Carditacea, and Leptonacea.

METABRANCHIA Ax, 1999

Reference: *Das System der Metazoa II*: 50, 51

Remarks: Established as a clade of the Bivalvia including all the bivalves except the Protobranchia, i.e. the Filibranchia plus Eulamellibranchia.

METARRHIPTAE Gill, 1871 [February]

Reference: *Smithsonian Miscellaneous Collections*, 227: 21

Remarks: Established as an order including the family Tridacnidae only.

MICROCILIOBRANCHIA Atkins, 1938 [May]

Reference: *Quarterly Journal of Microscopical Science*, new. ser., 80: 426, 430

Remarks: Established as a division of Lamellibranchia in which the latero-frontal tracts of the gill filaments consist characteristically of a row of micro-latero-frontal cilia, including the order Pseudolamellibranchia only, with the superfamilies Arcacea, Anomioidea, Pterioidea, Pectinoidea, and Ostreacea.

MICROPODA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 238

Remarks: Established as an order of the class Conchophora, including the genera *Pecten*, *Ostrea*, and *Anomia*.

MODIOMORPHOIDEA Newell, 1969

Reference: [in Moore, ed.] *Treatise on Invertebrate Paleontology*: 393

Remarks: Established as an order of Palaeoheterodonta, including the superfamilies Modiomorphoidea and Cycloconchoidea. Spelling and rank emended by Scarlato & Starobogatov (1978: 223) to suborder Modiomorphina (in synonymy of Actinodontina).

MONODONTEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 138

Remarks: Vernacular name only. Established as a division of the "Pleurodонтен" including the "Unioniden" only.

MONOMYARIA Lamarck, 1812

Reference: *Extrait du cours de zoologie du Muséum d'histoire naturelle*: 104

Remarks: Original spelling "monomyaires" (vernacular). Latinized as (suborder) Monomya by Menke (1828: 57); as Monomyaria by Zittel (1881: 16, 18). Established as a division of bivalves containing the "Brachiopodes", "Ostracées" and "Byssifères".

MONOSIPHONIPHORES Récluz, 1869

Reference: *Actes de la Société Linnéenne de Bordeaux*, 27(1): 30, table between pp. 34 and 35

Remarks: Vernacular name only. Established as an order of the subclass Dimyaria, including the "tribes" "Cratérodimaïres" (itself including the family Venericardiidae only) and "Cratéromonaïres" (itself including the families Crassatellidae, Scacchiidae, Carditidae, Ungulinidae, Mytilidae and Unionidae).

MONOTIDINA Waterhouse, 2001 [1 July]

Reference: *Late Paleozoic Brachiopoda and Mollusca from Wairaki Downs, New Zealand*: 134

Remarks: Established as a suborder of the order Pectinida including the superfamilies Monotoidea and Eurydesmoidea.

MUSCULITES Férussac, 1801

Reference: *Mémoires de la Société Médicale d'Emulation*, 4: 381

Remarks: Vernacular name only. Established as a class, containing the land and freshwater molluscs, both gastropods and bivalves.

MYACEA Stoliczka, 1870 [1 September]

Reference: *Memoirs of the Geological Survey of India. Palaeontologia Indica. Cretaceous fauna of southern India*, vol. 3, parts 1–4: 8b, 32

Remarks: Established as an order containing the family Myidae, Mactridae, Anatinidae, Saxicavidae, Glauconomyidae and Solenidae. Spelling and/or rank emended by P. Fischer (1887: 1112) to suborder Myacea; by Newell (1965: 20) to suborder Myina, including the superfamilies Myoidea, Gastrochaenoidea and Hiatelloidea.

MYALINACEA Paul, 1939

Reference: *Abhandlungen und Berichte aus dem Museum für Naturkunde und Vorgeschichte und dem Naturwissenschaftlichen Verein in Magdeburg*, 7(1): 169

Remarks: Established as a suborder of Filibranchia including the families Myalinidae, Modioloidea and Mytilidae.

MYOBRANCHIA Haeckel, 1902

Reference: *Natürliche Schöpfungsgeschichte*, ed. 10, *Theil* 2: 552

Remarks: Established as a division of the bivalve order Siphoniata.

MYOPHORELLINA M. R. Cooper, 1991

Reference: *Annals of the South African Museum*, 100(1): 9

Remarks: Established as a suborder of the order Trigonioidea, including the superfamilies Myophorelloidea and Megatrigonioidea.

MYOSTROPHA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 238

Remarks: A division of the class Conchophora, including the genera *Pholas*, *Teredo*, and *Aspergillum*. Spelling emended by Gray (1824b: 219) to *Myastropha*. Listed in error as a genus-group name by Sherborn, Neave and other nomenclators.

MYTILOIDA Férussac, 1822

Reference: *Tableaux systématiques des animaux mollusques*: xvii, xlii

Remarks: Original spelling “Les Mytillacés” (vernacular); established as an order including the families “Mytilacés”, “Nayades”, “Cardites” and “Crassatelles”. Latinized by Gray (1854a: 416) as suborder Mytilacea. Spelling and rank emended by Newell (in Moore, ed., 1969: 270) to order Mytiloida; by Scarlato & Starobogatov (1979a: 19) to superorder Mytiloida (in synonymy of Autobranchia); by Waterhouse (2008: 14) to superorder Mytilidia and order Mytilida.

NAIADACEA Dall, 1889 [December]

Reference: *The American Journal of Science*, ser. 3, 38: 460

Remarks: Established as a suborder of the order Prionodesmacea; contents not given. Used by White (1942: 40, 59) as equal to “Stirps Unionacea”, containing the families Unionidae and Etheriidae. Spelling and rank emended by Cox (1960: 85) to order Naiadida [declared new], containing the superfamilies Anthracosiacea and Unionacea.

NEOHETERODONTEI Taylor, Williams, Glover & Dyal, 2007 [November]

Reference: *Zoologica Scripta*, 36: 592, 594

Remarks: Established as an unranked clade containing the superfamilies Sphaeroidea, Myoidea, Pholadoidea, Dreissenoida,

Gaimardioidea, Mactroidea, Ungulinoidea, Corbiculoidea, Chamoidea, Veneroidea, plus the families Glossidae, Hemidonacidae, Glauconomidae, Trapezidae, Arcticidae, Vesicomidae, and Kelliellidae of unresolved superfamilial status.

NEOTAXODONTA Korobkov, 1954

Reference: *Spravochnik i metodicheskoe rukovodstvo po tretichnym molliuskam. Plastinchatozhabernye*: 57, 170

Remarks: Established as an order, as a substitute name for Prionodonta.

NEPIOMORPHIA Kříž, 2007 [November]

Reference: *Palaeontology*, 50(6): 1352, 1361

Remarks: Established as a superorder containing the orders Praecardioida and Antipleuroidea.

NUCINELLINA Scarlato & Starobogatov, 1971

Reference: [in Nevesskaja et al.] *Paleontologicheskii Zhurnal*, (1971): 12

Remarks: Established as suborder of the order Solemyida including the superfamilies Manzanelloidea and Huxleyoidea.

NUCULACEA Dall, 1889

Reference: *The American Journal of Science*, ser. 3, 38: 450, 460

Remarks: Established as a suborder of the order Prionodesmacea; contents not given. Spelling and rank emended by Newell (1965: 15) to order Nuculoida, containing the superfamilies Nuculacea and Nuculanacea; by Starobogatov (1992: 14, 20) to order Nuculiformes and superorder Nuculiformii.

NUCULANOIDA Carter, D. C. Campbell & M. R. Campbell, 2000 [12 December]

Reference: [in Harper, Taylor & Crame, eds.] *The evolutionary biology of the Bivalvia*: 61

Remarks: Established as an order including the superfamily Nuculanoidea. Also superorder Nuculaniformii (same reference) including the order Nuculanoida only.

OLIGODONTA March, 1912 [1 July]

Reference: *Annals and Magazine of Natural History*, ser. 8, 10(55): 101, 102

Remarks: Established as a division of Heterodonta, including the families Lucinidae, Astartidae, Condylardiidae, Cardiidae, Donacidae, Corbulidae, Tellinidae, Solenidae, Panopeidae, Pholadidae, Dreissenidae, and Trigonidae. Spelling and rank emended by Cox (1960: 85) to suborder Oligodontina.

OLIGOSYRINGIA Purchon, 1963 [January]

Reference: *Proceedings of the Malacological Society of London*, 35(2–3): 76

Remarks: Established as a subclass of the Bivalvia, including the orders Protobranchia and Septibranchia.

OPPONOBRANCHIA Giribet, 2008 [March]

Reference: *Phylogeny and evolution of the Mollusca*: 124

Remarks: Established as a clade of the Bivalvia, including the Nuculoida and Solemyoida.

ORTHOCONCHAE d'Orbigny, 1844

Reference: *Paléontologie française. Terrains crétacés*, 3: 14, 15

Remarks: Original spelling “Orthoconques” (vernacular). Latinized by Geinitz (1845: 394). Established as an order of Lamellibranchiata, including the suborders “Sinupaléales” and “Intégropaléales”. Rank emended by Gray (1854a: 414) to suborder.

ORTHONOTIA Pojeta, 1978 [16 November]

Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 284(1001): 230, 240

Remarks: Established as a subclass including the family Orthonotidae only. Spelling and rank emended by Morris, Dickins & Astafieva-Urbaitis (1991: 92) to order Orthonotoida.

OSTREOIDA Férussac, 1822

Reference: *Tableaux systématiques des animaux mollusques*: xxxix

Remarks: Original spelling “Les Ostracés” (vernacular). Established as an order containing the families “Les Rudistes”, “Les Huitres”, “Les Pectinides”, “Les Malléacés”, “Les Aviculés”, and “Les Arcacés”. Latinized by Gray (1854a: 418) as suborder Ostracea; also used by Gray (p. 418) as Ostreina, at rank between suborder (Ostracea) and family (Ostreidae and Placentidae). Spelling and rank emended by Iredale (1939: 391) to suborder Ostreiformes; by Waller (1978: 349, 352) to order Ostreoida and suborder Ostreina; by Waterhouse (2008: 182) to order Ostreidina.

PACHYDESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 146

Remarks: Vernacular name only. Established as a division of the bivalves including the “Panopaeen”.

PACHYDONTA Steinmann, 1903

Reference: *Einführung in die Paläontologie*: 234, 242

Remarks: Established as a division of Heterodonta of unspecified rank containing Monopleuridae, Caprinidae, Radiolitidae and Hippuritidae. Ranked by Moore (in Moore et al., 1952: 411) as order; spelling emended by Keen (1963: 91) to (order) Pachyodontida.

PACHYPODA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 237

Remarks: Established as an order of the class Conchophora, including the genera *Mya* and *Corbula*.

PALAEOBRANCHIA Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 232

Remarks: Established as an order including the family Solemyidae only. See also Lipodonta.

PALAEOCONCHAE Neumayr, 1884

Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, Abt. 1, 88(2): 392

Remarks: Established at the rank of order as a substitute name for “Cryptodonten” (vernacular), including *Solemya*.

PALAEOHETERODONTA Newell, 1965

Reference: *American Museum Novitates*, 2206: 18

Remarks: Established as a subclass including the orders Actinodontoida, Unionoida, and Trigonioida.

PALAEOLAMELLIBRANCHIA Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 305

Remarks: Established, at the rank of order, as a substitute name for Schizodonta, including the family Trigoniidae only. Ranked by Habe (1977: 112) as subclass (in synonymy of Palaeoheterodonta).

PALAEOMUTELINA Gusev, 1990

Reference: *Nemorskie dvustvorchatye molliuski verkhnnei Permi Evropeiskoi chasti SSSR*: 56

Remarks: Established as a suborder including the family Palaeomutelidae only.

PALAEOTAXODONTA Korobkov, 1954

Reference: *Spravochnik i metodicheskoe rukovodstvo pro tretichnym molliuskam. Platinchatozhabernye*: 56, 72

Remarks: Established as an order of the class Lamellibranchiata, containing the families Nuculidae, Nuculanidae (= Ledidae), and Malletiidae. Spelling and rank emended by Cox (1960: 85) to order Palaeotaxodontida; by Keen (1963: 90) to suborder Palaeotaxodontida; by Newell (1965: 15, 16) to subclass Palaeotaxodonta, containing the order Nuculoida. See also Ctenidiobranchia.

PANDORACEA Stewart, 1930 [9 August]

Reference: *The Academy of Natural Sciences of Philadelphia, Special Publication*, 3: 26

Remarks: Established, at the rank of order, as a substitute name for Anatinacea. Spelling and rank emended by Iredale (1939: 231) to suborder Pandoriformes.

PANTODONTA Dall, 1895 [March]

Reference: *Transactions of the Wagner Free Institute of Philadelphia*, 3(3): 537

Remarks: Established as a division of the order Teleodesmacea containing the family Allodesmatidae only. Spelling emended by Cox (1960: 85) to Pantodontida.

PARAFILIBRANCHIA Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 306, 403

Remarks: Established as an order of the subclass Prionodesmacea, including the families Anomiidae and Placunidae. Ranked by Habe (1977: 97) as superfamily (in synonymy of Anomiacea).

PARALLELODONTEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 140

Remarks: Vernacular name only. Established as a division of the bivalves including the “Synmyarier” family “Tridacniden” and the “Dimyarier” families “Chamiden” and “Carditiden”.

PATULIPALLA Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: 331

Remarks: Established as an order containing the “sections” “Mésomyones” and “Plagimyones”.

PECTINACEA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13: 417

Remarks: Established as an order containing the suborders Arcacea (Trigoniidae and Arcidae), Malleacea (Pteriidae), and Ostracea (Spondylidae, Pectinidae, Limidae, Ostreidae, Placenticidae, and Anomiidae). Also used by Gray (p. 418) as Pectinina, at rank below suborder (Ostracea) and above family (includes Spondylidae, Pectinidae and Limidae). Spelling and/or rank emended by P. Fischer (1886: 935) to suborder Pectinacea; by Iredale (1939: 344) to suborder Pectiniformes; by Waller (1978: 353) to suborder Pectinina [declared new]; by Nevesskaja et al. (1971: 13) to order Pectinida; by Carter (1990: 234) to order Pectinoida; by Waterhouse (2008: 39) to superorder Pectinidia.

PELECYPODA Goldfuss, 1820

Reference: *Handbuch der Zoologie*, 1: 599

Remarks: Established as an order, including the families Ostracea, Byssifera, Tridacnae, Aviculae, Arcacea, Mytilacea, Myacea, and Cardiacea. See also Cormopoda. Ranked by Philippi (1853: 298) as class (in synonymy of Conchifera).

PELICOIDEA Menke, 1828

Reference: *Synopsis methodica molluscorum*: 65

Remarks: Established as an order of the class Elatobranchiata, containing the family Tridacnidae only.

PERICLISTA Burmeister, 1837

Reference: *Handbuch der Naturgeschichte*, 2: v, 489

Remarks: Established as a division of the order Cormopoda (= bivalves), including the families Teredinidae and Aspergillidae.

PHOLADACEA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 414

Remarks: Established as an order of the subclass Siphonophora containing the suborders Orthoconchae and Heteroconchae. Spelling and/or rank emended by Hescheler (1900: 24) to suborder Pholadacea; by Newell (1965: 21) to suborder Pholadina [declared new].

PHOLADOMYOIDA Newell, 1965

Reference: *American Museum Novitates*, 2206: 21

Remarks: Established as an order of the subclass Anomalodesmata, including the suborders Clavagellina and Pholadomyina, itself including the superfamilies Pholadomyoidea [= Pholadomyidae, Burmesidae, Ceratomyidae, and Pleuromyidae] and Pandoroidea [= Pandoridae, Cleidothaeridae, Laternulidae, Lyonsiidae, Myochamidae, Periplomatidae, and Thraciidae].

PHYLLOPODA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 237

Remarks: Established as an order of the class Conchophora, including the genera *Solen*, *Psammobia*, *Tellina*, *Cyclas*, *Venus*, *Cardium*, *Tridacna*, *Chama*, *Pectunculus*, *Trigonia*, and *Unio*.

PINNIFORMES Iredale, 1939 [25 February]

Reference: *Great Barrier Reef Expedition 1928–29. Scientific Reports*, 5(6): 306

Remarks: Established as a suborder of the order Pseudolamellibranchia, including the families Pinnidae and Philobryidae. Spelling emended by Moore (in Moore et al., 1952: 411, 430) to Pinnacea; by Waller (1978: 351) to Pinnina [declared new suborder], including the superfamily Pinnoidea.

PISIDIOINEI Starobogatov, 1992

Reference: *Ruthenica*, 2(1): 22, 23

Remarks: Established as an infraorder of the suborder Astartoidei, including the families Euperidae, Sphaeriidae, Pisidiidae, and Euglesidae.

PLAGIMYONA Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: 331, table

Remarks: Original spelling “Plagimyones” (vernacular). Latinized by Berthold (1827: 202). Established as a division of the order Patulipalla, containing the family “Arcacés” only.

PLATODESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 139

Remarks: Vernacular name only. Established as a division of the “Taxodonten” bivalves including the “Arciden” only.

PLEUROCONCHAE d’Orbigny, 1844

Reference: *Paléontologie française. Terrains crétacés*, 3: 15

Remarks: Original spelling “Pleuroconques” (vernacular). Latinized by Geinitz (1845: 456). Established as an order containing the families Aviculidae, Pectinidae, Spondylidae, Chamiidae, Etheridae, Ostreidae and Anomiidae.

PLEURODONTA March, 1912 [1 July]

Reference: *Annals and Magazine of Natural History*, ser. 8, 10(55): 101, 102

Remarks: Established as an order including the suborders Dysodonta and Taxodonta. The composition is thus different from that of the “Pleurodонтен” of Vest (see below), and Pleurodonta of March is not a latinization of the latter.

PLEURODONTEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 138

Remarks: Vernacular name only. Established as a division of the bivalves including the “Monodonten”, “Rhipidodonten”, “Anodonten” (itself including “Anodontiden” only), and “Polydонтен”.

PLIODONTA March, 1912 [1 July]

Reference: *Annals and Magazine of Natural History*, ser. 8, 10(55): 101, 102

Remarks: Established as a division of the order Heterodonta, containing the families Mactridae, Scrobicularidae, Mesodesmatidae, Cuspidariidae, Cardiliidae, Anatinidae, Cuspidariidae, Cyrenidae, Rangiidae, Veneridae, Cyprinidae, Isocardiidae, Petricolidae, Erycinidae, Kelliellidae, Chamidae, Rudistae, and Diceratidae. Spelling and rank emended by Cox (1960: 85) to suborder Pliodontina.

POGONOPODA Gray, 1821 [1 March]

Reference: *London Medical Repository*, 15(87): 237

Remarks: Established as an order of the class Conchophora, including the genera *Arca*, *Mytilus*, and *Avicula*.

POLYDESMEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 136

Remarks: Vernacular name only. Established as a division of the bivalves including the “Perniden”.

POLYDONTEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 139

Remarks: Vernacular name only. Established as a division of the “Pleurodonten” bivalves including the “Muteliden” only.

POLYSYRINGIA Purchon, 1963 [January]

Reference: *Proceedings of the Malacological Society of London*, 35(2–3): 76

Remarks: Established as a subclass of the class Bivalvia, including the orders Gastrot-riteia, Gastrotetartika, and Gastropempta.

POROMYACEA Ridewood, 1903 [31 January]

Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 187, 265

Remarks: Established as a suborder including the families Verticordiidae, Poromyidae, Cetoconchidae, and Cuspidariidae. Spelling and rank emended by Newell (1965: 21) to order Poromyoida.

PRAECARDIOIDA Newell, 1965

Reference: *American Museum Novitates*, 2206: 17

Remarks: Established as an order including the superfamilies Praecardioidea and Edmondioidea. Spelling and rank emended by Scarlato & Starobogatov (1979a: 20) to suborder Praecardiina (in synonymy of Pteriina).

PRAEHETERODONTA Douvillé, 1912

Reference: *Comptes Rendus des Séances de l'Académie des Sciences*, 154: 1681, 1682

Remarks: Original spelling “Préhétérodontes” (vernacular). Latinized by Cossmann (1913: 215, 252) [and listed in error in *Nomenclator Zoologicus* as a genus-group name]. Division of Taxodonta including the families “Myophoridés” and “Préastartidés”. Ranked by Davies (1935: 130) as order. Spelling emended by Scarlato & Starobogatov (1969: 8) to (order) Praeheterodontida.

PRIONODESMACEA Dall, 1889

Reference: *American Journal of Science*, ser. 3, 38: 453, 460

Remarks: Established as an order containing the suborders Nuculacea, Arcacea, Naia-dacea, Trioniacea, Mytilacea, Pectinacea, Anomiacea and Ostracea. Spelling and/or rank emended by Winckworth (1932: 239) to subclass Prionidesmacea; by Keen (1963: 90) to subclass Prionodesmata.

PRIONODONTA MacNeil, 1937 [15 November]

Reference: *Journal of the Washington Academy of Sciences*, 27(11): 457

Remarks: Not available from the vernacular and informal “prionodont” of Dall (1889b: 453). Established by MacNeil as a suborder of the order Filibranchia, including the superfamilies Cyrtodontoidea, Parallelodontoidea, Glycymeroidea and Arcoidea. Rank emended by Nicol (1966: 18) to order; by Amler (1999: 239) to superorder. See also Neotaxodonta.

PROSPONDYLOIDINA Waller, 2005 [January]

Reference: [in Waller & Stanley] *Journal of Paleontology*, 79(1, suppl.): 47

Remarks: Established as a suborder of Pectinoida including the families Prospondylidae, Plicatulidae, Anomiidae, and Dimyidae.

PROTOBRANCHIATA Pelseneer, 1889 [April]

Reference: *Bulletin Scientifique de la France et de la Belgique*, 20: 50–52

Remarks: Original spelling “Protobranchiés” (vernacular); latinized by Grobben (1892a: 142; 1892b: 373). Established as an unranked division of Pelecypoda, including Nuculidae and Solemyidae; ranked by Grobben as subclass; by Cooke (in Harmer & Shipley, eds., 1895: 447) as order. Spelling emended by Hescheler (1900: 64) to Protobranchia. See also Gastroproteia.

PROTOCONCHAE Hertwig, 1895

Reference: *Lehrbuch der Zoologie*, ed. 3: 323

Remarks: Original spelling “Protoconchen” (vernacular). Latinized by Hertwig (1903: 335). Established as an order including the “Dimyarier” and the “Anisomyarier”.

PSEUDOCTENODONTA Dechaseaux, 1952

Reference: [in Piveteau, ed.] *Traité de paléontologie*, 2: 261, 271

Remarks: Original spelling Pseudo-Ctenodonta. Established as a suborder containing the families Arcidae and Parallelodontidae. Spelling and rank emended by Babin (1966: 142) to order Pseudectenodontida.

PSEUDOLAMELLIBRANCHIATA Pelseneer, 1889 [April]

Reference: *Bulletin Scientifique de la France et de la Belgique*, 20: 50–52

Remarks: Original spelling “Pseudolamelibranchiés” (vernacular); latinized by Cooke (in Harmer & Shipley, eds., 1895: 449). Established as a division of Pelecypoda, including Mytilacea, Pectinacea, and Ostracea; ranked by Cooke as an order. Spelling emended by

Winckworth (1932: 240) to Pseudolamel-
libranchia, including the families Pteriidae,
Ostreidae, Pinnidae, and Limidae.

PTERINOPECTINIDA Waterhouse, 2008 [28 March]

Reference: *Earthwise*, 8: 43

Remarks: Established as an order including
the superfamilies Leiopectinoidea, Pteri-
nopectinoidea, Halobioidea, and the family
Permanomiidae of unresolved superfamily
allocation.

PTERIOIDA Newell, 1965

Reference: *American Museum Novitates*, 2206:
17

Remarks: Established as an order including
the suborder Pteriina only, itself including the
superfamilies Ambonychioidea, Pterioidea,
Pectinoidea, Anomioidea, and Limoidea. Spell-
ing and rank emended by Polubotko (1980: 50)
to suborder Pteriina; by Waterhouse (2008:
18) to superorder Pteriidia, order Pteriida, and
suborder Pteriidina.

PTERIOMORPHA Beurlen, 1944

Reference: *Sitzungsberichte der Mathematisch-
Naturwissenschaftlichen Abteilung der Bay-
erischen Akademie der Wissenschaften zu
München*, 1944(1–2): 144

Remarks: Established as an order including
the family-groups Pteriacea, Pectinacea, Os-
treacea, Anomiacea, Mytilacea, and Arcacea.
Spelling and rank emended by Cox (1960: 85)
to subclass Pteriomorphia, including the orders
Eutaxodontida, Pteroconchida, Colloconchida,
Isofilibranchia, and Rostroconchida; by Waller
(1978: 351) to superorder Pteriomorphia.

PTEROCONCHIDA Cox, 1960

Reference: *Proceedings of the Malacological
Society of London*, 34(2): 85

Remarks: Established as an order of the
subclass Pteriomorphia, including the super-
families Pterioidea, Pinnoidea, Pectinoidea,
Limoidea, and Anomioidea. Spelling and rank
emended by Scarlato & Starobogatov (1969:
8) to suborder Pteroconcha.

PTYCHOBANCHIA Haeckel, 1902

Reference: *Natürliche Schöpfungsgeschichte*,
ed. 10, *Theil* 2: 552

Remarks: Established as a division of the bivalve
order Asiphonia.

RADIIDENTINA Scarlato & Starobogatov, 1975

Reference: *Vsesoiuznoe soveshchanie po
izucheniiu molliuskov*, 5: 4

Remarks: Established as suborder of the order
Ctenodontida, including the superfamilies
Phaseoloidea and Radiidentoidea.

RHIPIDODONTEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen
des Siebenbürgischen Vereins für Naturwis-
sensschaften zu Hermannstadt*, 48: 139

Remarks: Vernacular name only. Established
as a division of the “Pleurodонтен” bivalves
including the “Hyriiden” only.

ROSTROCONCHIDA Cox, 1960 [August]

Reference: *Proceedings of the Malacological
Society of London*, 34(2): 85

Remarks: Established as an order of the bi-
valve subclass Pteriomorpha, including the
superfamily Conocardioidea only. Rank and
spelling emended to class Rostroconchia by
Pojeta et al. (1972: 264).

RUDISTA Blainville, 1825

Reference: *Manuel de malacologie et de con-
chyliologie*: 516

Remarks: Established as an order of Acepha-
lophora including the genera *Spherulites*,
Hippurites, *Radiolites*, *Birostrites*, and *Cal-
ceola*. Spelling and rank emended by Moore
(in Moore et al., 1952: 411, 440) to suborder
Rudistacea. See also family list.

SAXICAVOIDEA Morretes, 1949

Reference: *Arquivos do Museu Paranaense*,
7: 47

Remarks: Established as a suborder including
the family Saxicavidae only.

SCHIZODONTA Steinmann, 1888

Reference: [in Steinmann & Döderlein] *Elemen-
te der Paläontologie*, 1: 238, 250

Remarks: Established as an order including
the family Trigoniidae only. Ranked by Haas
(1929: 16) as suborder. See also Palaeo-
lamellibranchia.

SCOLIÉPHORES Récluz, 1869

Reference: *Actes de la Société Linnéenne de
Bordeaux*, 27(1): 31, table between pp. 34
and 35

Remarks: Vernacular name only. Established
as a suborder of the order “Disiphonipho-
res”, including the “tribes” “Cratéromonai-
res” (including the families Aspergillidae,
Pholadidae, Gastrochaenidae, Solenidae,
Panopaeidae, Glycymeridae, Ceromyidae,
Myidae, Pandoridae, Anatinidae, Mactridae,
and Amphidesmatidae) and “Cratérodimai-

res" (including the families Lavignonidae, Mesodesmatidae, Ledidae, Malletiidae, Tellinidae, Psammobiidae, Tapetidae, Veneridae, Cyrenidae, and Iridinidae).

SEPTIBRANCHIA Pelseneer, 1888

Reference: *Comptes-Rendus des Séances de l'Académie des Sciences*, 106: 1031

Remarks: Established as a name above family, containing Poromyidae and Cuspidariidae. Spelling emended to Septibranchiata by Cooke (1895: xi, 459). Rank emended by Suter (1913: 1035) to order; by Nevesskaja et al. (1971: 18) to superorder; by Allen & Morgan (1981: 418) to suborder. See also Gastrodeuteia and Septipalliata.

SEPTIPALLIATA Hescheler, 1900

Reference: [in Lang, ed.] *Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere*, ed. 2, vol. 3: 25

Remarks: Established in synonymy of, and as a substitute name for, Septibranchia.

SINISTRODONTA Pchelintsev, 1959

Reference: *Geologicheskii Muzei Karpinskogo, Seriya Monograficheskaya*, 3: 160

Remarks: Established as a suborder. Treated by Eberzin (1960: 155) as a superfamily and not available as such (not based on a genus).

SINUPALLIATA d'Orbigny, 1844

Reference: *Paléontologie française. Terrains crétacés*, 3: 14, 299

Remarks: Original spelling "Sinupalléales" (vernacular). Established as a suborder containing Clavagellidae, Pholadidae, Solenidae, Anatinidae, Tellinidae, Petricolidae, Cythereidae and Corbulidae. Latinized by S. P. Woodward (1854: 252) as Sinu-pallialia; and by Zittel (1881: 17, 108) as Sinupalliata.

SIPHONIDA J. Fleming, 1828 [March]

Reference: *A history of British animals*: 408

Remarks: Taxon containing the families of bivalves with siphons, also including Mytilidae and Unionidae. Treated by Zittel (1881: 17, 63) as an order including the families of bivalves with siphons, but excluding Mytilidae and Unionidae. See also Siphonidae in family list.

SIPHONOPHORA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 409

Remarks: Established as a subclass of the class Conchifera including the orders Veneracea and Pholadacea.

SOLEMYACEA Dall, 1889

Reference: *The American Journal of Science*, ser. 3, 38: 457, 460

Remarks: Original spelling Solenomyacea. Established as a suborder, contents not specified. Spelling and/or rank emended by J. Morton (1963: 64) to order Solenomyacea; by Newell (1965: 7, 17) to order Solemyoida.

SOLENACEA Dall, 1889 [December]

Reference: *The American Journal of Science*, ser. 3, 38: 460

Remarks: Established as a suborder of the order Teleodesmacea. No contents given.

SPONDYLACEA Moore, 1952

Reference: [in Moore et al.] *Invertebrate fossils*: 411, 422

Remarks: Established as a suborder of Isodonta; family composition not given, but *Spondylus* and *Plicatula* cited as examples.

SUBFILIBRANCHIATA Cossmann & Peyrot, 1909

Reference: *Actes de la Société Linnéenne de Bordeaux*, 63(2): 100

Remarks: Established as a suborder of Anisomyaria including Mytilacea and Anomiacea.

SUBFOLIOBRANCHIA Scarlato & Starobogatov, 1969

Reference: *Soveshchanie po probleme "Puti i zakonomernosti istoricheskogo razvitiia zhivotnykh i rastitelnykh organizmov"*: 8

Remarks: Attributed by Scarlato & Starobogatov to "Lang, 1900". Hescheler (in Lang, ed., 1900: 142) had used "subfoliobranchiaten" as an adjective. Established by Scarlato & Starobogatov as an order of Septibranchia including the superfamily Verticordioidea only.

SUBMYTILACEA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 416

Remarks: Established as a suborder of the order Unionacea, including the families Carditidae, Crassatellidae, Unionidae and Etheriidae.

SUBSILIENTIA Poli, 1791

Reference: *Testacea Utriusque Siciliae*, 1: 27; 2: 251 [1795]

Remarks: Established as a subdivision of *Mollusca testacea*, or used as an adjective meaning “jumping”, as opposed to those molluscs that are crawling or are branched. Includes various bivalves [e.g., *Hypogaea*, *Cerastes*, *Loripes*, *Axinaea*].

SYNAPTORHABDA Ridewood, 1903 [31 January]
Reference: *Philosophical Transactions of the Royal Society of London*, ser. B, 195: 186
Remarks: Established as an order including “the orders Eulamellibranchia and Septibranchia of Pelseneer, together with the genera *Pinna*, *Lima* and *Ostrea*”.

SYNDESMEN Vest, 1899
Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 136
Remarks: Vernacular name only. Established as a division of the bivalves including the “Monomyarier” family “Ostreiden”, the “Anisomyarier” family “Pteriaceen”, and the “Dimyarier” family “Aetheriiden”.

SYNMYARIER Vest, 1899
Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 141
Remarks: Vernacular name only. Established as a division of the “Parallelodonten” bivalves including the “Tridacniden” only.

TAXODONTA Neumayr, 1884
Reference: *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften*, Abt. 1, 88(2): 412
Remarks: Original spelling “Taxodonten” (vernacular). Latinised by P. Fischer (1886: 921). Established as an order including the families Arcidae and Nuculidae. Ranked by Abbott (1954: 341) as suborder.

TELEODESMACEA Dall, 1889
Reference: *American Journal of Science*, ser. 3, 38: 453, 460
Remarks: Established as an order containing the suborders Tellinacea, Solenacea, Mactracea, Carditacea, Cardiacea, Chamacea, Tridacnacea, Veneracea, Lucinacea, and also with doubt Leptonacea, Isocardiacea, and Rudista. Spelling and/or rank emended by Winckworth (1932: 242) to subclass Teleodesmacea; by Keen (1963: 91) to subclass Teleodesmata.

TELEODONTA Dall, 1895 [March]
Reference: *Transactions of the Wagner Free Institute of Philadelphia*, 3(3): 551
Remarks: Established as a division of the order Teleodesmacea containing the superfamilies Veneracea, Solenacea, Tellinacea and Mactracea. Spelling and rank emended by Keen (1963: 91) to suborder Teleodontida.

TELLINACEA Stoliczka, 1870 [1 September]
Reference: *Memoirs of the Geological Survey of India. Palaeontologica Indica. Cretaceous Fauna of Southern India*, vol. 3, parts 1–4: 8b, 28
Remarks: Established as order containing the families Paphiidae [= Mesodesmatidae], Scrobiculariidae and Tellinidae. Ranked by Hescheler (1900: 23) as suborder containing the families Tellinidae, Donacidae and Mactridae.

TENUIPEDA Lamarck, 1818
Reference: *Histoire naturelle des animaux sans vertèbres*, 5: 423, 425, 465
Remarks: Original spelling “Tenuipèdes” (vernacular), established as a division (pp. 423) or section (p. 425) of the “Dimyaires”, including “les Mactracées, les Corbulées, les Lithophages, les Nymphacées”. Latinized by Children (1822: 85, as Tenuipeda; same composition as Lamarck’s) and Burmeister (1837: v, 486, as Tenuipedia) as a division of the Dimyia, including the families “Nymphacea”, “Lithophaga”, Corbulidae, and Mactridae.

TETRABRANCHIA Blainville, 1814 [2 November]
Reference: *Bulletin des Sciences par la Société Philomatique de Paris, Zoologie*, (1814): 179
Remarks: Original spelling “Tétrabranche” (vernacular). Latinized by P. Fischer (1886: 923). Established, at the rank of order, as a substitute name for “Acéphalés”.

TRIDACNACEA Dall, 1889 [December]
Reference: *The American Journal of Science*, ser. 3, 38: 460
Remarks: Established as a suborder of the order Teleodesmacea. Contents not given.

TRIFORIPALLA Latreille, 1824
Reference: *Annales des Sciences Naturelles*, 3: 332, table
Remarks: Established as an order including the family Tridacnidae only.

TRIGONIOIDA Dall, 1889

Reference: *The American Journal of Science*, ser. 3, 38: 460

Remarks: Established as a suborder of the order Prionodesmacea; contents not given. Spelling and rank emended by Steinmann (1903: 234) to Trigoniacea [rank above family]; by Newell (1965: 16, 18) to order Trigonioida, containing the families Trigoniidae, ?Lyrodesmatidae, Myophoriidae, ?Scaphellinidae, and ?Trigonioiidae.

TRIMYA Leach, 1852

Reference: *A synopsis of the Mollusca of Great Britain*: 353

Remarks: Established as an order including the family Anomiidae only.

TRIODONTEN Vest, 1899

Reference: *Verhandlungen und Mittheilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 48: 144

Remarks: Vernacular name only. Established as a division of the bivalves including the "Astarten" and "Veneriden".

TROPIOPODA Reeve, 1841

Reference: *Conchologia systematica*: table

Remarks: Established as a class, including the orders Bimusculosa and Unimusculosa, together comprising all the bivalves.

TUARANGIIDA MacKinnon, 1982 [29 April]

Reference: *Journal of Paleontology*, 56(3): 591

Remarks: Established as an order of the subclass Pteriomorpha, including the superfamily Tuarangioidea, itself including the family Tuarangiidae only.

TUBICOLA Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: 332, table

Remarks: Original spelling "Tubicoles" (vernacular). Latinized by Berthold (1827: 213). Established as a division of Tubipalla, containing the family Teredinidae only.

TUBIPALLA Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: 331, table

Remarks: Established as an order, including the divisions "Uniconques" and "Tubicoles".

UNICONCHAE Latreille, 1824

Reference: *Annales des Sciences Naturelles*, 3: 332, table

Remarks: Original spelling "Uniconques". Latinized by Berthold (1827: 207). Established as a division of Tubipalla containing the subdivisions "Clausiconques" and "Hianticonques".

UNIMUSCULOSA Reeve, 1841

Reference: *Conchologia systematica*: table

Remarks: Established as an order of the class Tropiopoda, containing the families Tridacnacea, Mytilacea, Aviculacea, Pectinacea, and Ostracea.

UNIONACEA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 415

Remarks: Established as an order of the subclass Siphonophora containing the suborders Lucinacea (Lucinidae), Submytilacea (Carditidae, Crassatellidae, Unionidae, Etheriidae), and Mytilacea (Mytilidae, Pinidae). Spelling and/or rank emended by Newell (1965: 16, 18) to order Unionoida; by Scarlato & Starobogatov (1979a: 19) to suborder Unionina.

VENERACEA Gray, 1854 [1 May]

Reference: *Annals and Magazine of Natural History*, ser. 2, 13(77): 410

Remarks: Established as an order, including the families Veneridae, Cyprinidae, Glauconomidae, Petricolidae, Tellinidae, Mactridae, Glossidae, Anatinidae, Cardiidae, Ledidae, Dreissenidae, and Tridacnidae. Spelling and/or rank emended by Dall (1889b: 460) to suborder Veneracea; by Newell (1965: 19) to order Veneroida; by Scarlato & Statobogatov (in Nevesskaja et al., 1971: 17) to order Venerida and suborder Venerina.

VERTICORDIIDA Scarlato & Starobogatov, 1971

Reference: [in Nevesskaja et al.] *Paleontologicheskii Zhurnal*, 1971(2): 19

Remarks: Established as an order, including the families Lyonsiellidae, Verticordiidae, and Euciroidae. Spelling and rank emended by Scarlato & Starobogatov (1983: 9) to order Verticordiiformes and suborder Verticordioidei.

Part 2. CLASSIFICATION OF BIVALVE FAMILIES

Rüdiger Bieler, Joseph G. Carter & Eugene V. Coan

Purpose, Rationale and Conventions

Historically, the purpose of biological classifications had primarily been to organize the large numbers of taxonomic names for living (and, where applicable, fossil) organisms in a hierarchical system where they could be found and retrieved. Later, it became accepted that classifications should reflect the evolutionary history of the treated group, so that biological and ecological attributes and properties could be predicted for a taxon from its position in the classification based on morphological and/or molecular characters. Classifications currently used by malacologists are often hybrids of different schools and traditions, with the working classification presented below no exception.

There is much debate in the scientific community on biological classifications, with special focus on such controversial issues as ranks and hierarchy. The present work is not the place to enter this theoretical debate. It has been our challenge to place all family-group names covered by the Nomenclator into a working ranked classification that can provide a roadmap capable of addressing questions and issues that an alphabetically arranged Nomenclator cannot: is family name X currently considered valid and to what larger unit does it belong? If it is not currently considered a valid name, where does it fall into synonymy according to current literature knowledge? How is nomenclatural priority affected by the numerous revisions of author/date citations in the Nomenclator? In some cases, we discovered problems that will need applications to the ICZN to resolve – we have annotated such issues in our footnotes.

For the best of all reasons – active anatomical, molecular, and paleontological research focusing on aspects of phylogenetic systematics in this group – “bivalve classification” remains a moving target. Recent molecular studies have given novel insight into relationships, questioned traditional placements of family-group and ordinal taxa, and led to the introduction of new names for hypothesized larger clades. Much of this work has yet to be reconciled with conflicting morphological data and, especially, placed into context of the fossil record. Several larger-scale projects in this direction are currently underway – most notably the projects

revising the Bivalvia content of the *Treatise on Invertebrate Paleontology* (www.paleo.ku.edu/treatise) and the Bivalve Tree-of-Life project (www.bivatol.org). The present publication is thus intended as a technical tool and nomenclatural foundation for future projects.

The following conventions have been used:

(a) Higher Groups and Ranking

To provide a widely accessible roadmap that reflects usage in both neontological and paleontological literature, we have used only a small number of categories above the ordinal level. The Bivalvia are here divided into two subclasses, Protobranchia (= Palaeotaxodonta) and Autobranchia, with the latter organized into Superorders Nepiomorphia, Pteriomorphia, and Heteroconchia. Because of the still widely accepted and fairly stable use of ordinal names in Bivalvia (much in contrast to current usage in Gastropoda), we have employed traditional orders to group the recognized superfamilies. We are fully aware that these “orders” do not necessarily represent monophyletic clades (it appears, for instance, that the Ostreida are derived from within the Pteriida). In view of the currently limited resolution of bivalve relationships and the large number of poorly known extinct taxa that may or may not be stem groups of certain living members, it appears more useful to retain paraphyletic groups than to abandon any signal of relationship.

(b) Lumping vs. Splitting

In some instances, the working classification of a family uses subfamilies and tribes, which may give an impression of a well-resolved analysis of that family. This is often not the case, but the alternative would have been to treat all included names as synonyms. As it will be easier to lump than to split as knowledge improves, we have chosen to present highly dissected classifications in situations in need of re-evaluation. In some cases, especially when the group had no history of subfamilies and tribes, we have placed poorly known and/or controversial families as junior synonyms of other families, or as *incertae sedis* within

the most appropriate higher taxon. We want to emphasize that these should be seen as hypotheses to be tested, rather than a reflection of detailed knowledge of the families in question.

In some cases when we have felt that the classification of a particular superfamily was built on a highly unstable foundation, with non-parallel or single minor characters used to elevate various families, and lack of molecular characters for most members, we have adopted a conservative course and listed many family and subfamily names as synonyms, as with the Galeommatoidea.

(c) Uncertainties and Question Marks

We indicate uncertain placement of taxa in most cases by using “[rank] uncertain.” For instance, the family Hemidonacidae is placed as “Superfamily uncertain” with the Veneroida. In a few cases, when our hypothesized placement of a taxon name is especially tentative, we employ question marks. This should not give the impression that an allocation or a synonymy without a question mark has been established beyond doubt. Again, we wish to emphasize that the working classification represents current understanding and/or an educated guess to be tested.

(d) Entirely Extinct Taxa

The dagger (†) sign before a taxon denotes that all members of that taxon are fossils.

(e) Ordering

In view of the often poorly resolved situation within subclades of the bivalve tree, and to avoid lengthy discussions of conflicting signals and opinions that would exceed the goals of this technical listing, we have opted for alphabetical arrangements of superfamilies within orders. This results in a listing that differs from published arrangements that are meant to reflect relationship. The alphabetized portions of our classification embody no such hypotheses and should not be seen as “overruling” such prior efforts. Within a superfamily, the nominate family is given first, then all other families in alphabetical order; the same convention applies to subfamilies within a family, and to tribes within a subfamily. After each valid family-group name, synonyms are presented in chronological order of their establishment (names introduced in the same publication are secondarily ordered

by alphabet). For completeness, we have also listed names in the synonymy that are “not available” or “permanently invalid”; such names are marked by “(n.a.)” or “(invalid),” respectively.

(f) Rank Abbreviations

SPF	Superfamily
SF	Subfamily
T	Tribe
ST	Subtribe

Class Bivalvia Linnaeus, 1758

Subclass, Order, and SPF uncertain

- †Family ARCHAEOCARDIIDAE Khalfin, 1940
- †Family CAMYIDAE Hinz-Schallreuter, 2000
- †Family CARDIOLARIIDAE Cope, 1997
- †Family CIRRAVIDAE Chernyshev, 1935
- †Family FORDILLIDAE Pojeta, 1975
- †Family LAURSKIIDAE Khalfin, 1948
- †Family THORALIIDAE N. J. Morris, 1980
- †Family TUARANGIIDAE MacKinnon, 1982

Subclass Protobranchia Pelseneer, 1889¹ [= Palaeotaxodonta Korobkov, 1954]

Order and SPF uncertain

- †Family AFGHANODESMATIDAE Scarlato & Starobogatov, 1979
- †Family ANTACTINODIONTIDAE Guo, 1980
- †Family CTENODONTIDAE Wöhrmann, 1893
- †Family ERITROPIDAE Cope, 2000
- †Family PSEUDOCYRTODONTIDAE Mailieux, 1939
- †Family TIRONUCULIDAE Babin, 1982 [= Natasinae Sánchez, 1997]

¹ Although the original spelling was Protobranchiata, the spelling Protobranchia in prevailing usage is followed here.

Order Nuculida Dall, 1889**SPF NUCULOIDEA GRAY, 1824**

Family NUCULIDAE Gray, 1824

SF NUCULINAE Gray, 1824

SF NUCULOMINAE Maxwell, 1988

†SF PALAEONUCULINAE Carter, 2001

†Family NUCULARCIDAE Pojeta & Stott, 2007

†Family PALAEOCONCHIDAE S. A. Miller, 1889

†Family PRAENUCULIDAE McAlester, 1969 [= Concavodontinae Sánchez, 1999]

Family SAREPTIDAE Stoliczka, 1870

SF SAREPTINAE Stoliczka, 1870 [= Setiglominae Schileyko, 1983²]

SF PRISTIGLOMINAE Sanders & Allen, 1973 [= Glominae Verrill & Bush, 1897 (invalid)]

Order Solemyida Dall, 1889**SPF MANZANELLOIDEA Chronic, 1952**

Family MANZANELLIDAE Chronic, 1952 [= Nuculinidae Chronic, 1952 (invalid); = Nucinellidae H. A. Vokes, 1956; = Huxleyiidae Scarlato & Starobogatov, 1971]

SPF SOLEMYOIDEA Gray, 1840

Family SOLEMYIDAE Gray, 1840

SF SOLEMYINAE Gray, 1840 [= Janacekiidae Růžicka & Řehoř, 1978]

SF ACHARACINAE Scarlato & Starobogatov, 1979

†SF CLINOPISTHINAE Pojeta, 1988

Order Nuculanida Carter, D. C. Campbell & M. R. Campbell, 2000**SPF NUCULANOIDEA H. Adams & A. Adams, 1858 (1854)**Family NUCULANIDAE H. Adams & A. Adams, 1858 (1854) [= Ledidae Gray, 1854³]

SF NUCULANINAE H. Adams & A. Adams, 1858 (1854) [= Adranidae Scarlato & Starobogatov, 1979; = Poroledidae Scarlato & Starobogatov, 1979; = Zealedidae Scarlato & Starobogatov, 1979]

SF LEDELLINAE Allen & Sanders, 1982 [= Parayoldiellinae Filatova & Schileko, 1984]

Family BATHYSPINULIDAE Coan & Scott, 1997⁴ [= Spinulinae Allen & Sanders, 1982 (invalid)]

†Family CADOMIIDAE Scarlato & Starobogatov, 1979

†Family CUCULLELLIDAE P. Fischer, 1886 [= Nuculitidae Bradshaw, 1999]

†Family ISOARCIDAE Keen, 1969

Family MALLETIIDAE H. Adams & A. Adams, 1858 (1846) [= Solenellidae d'Orbigny, 1846⁵; = Strabinae Prantl & Růžicka, 1954]

Family NEILONELLIDAE Schileyko, 1989 [= Saturniidae Allen & Hannah, 1986 (invalid)]

†Family PALAEOONEILIDAE Babin, 1966

Family PHASEOLIDAE Scarlato & Starobogatov, 1971 [= Lametilidae Allen & Sanders, 1973]

†Family POLIDEVCIIDAE Kumpera, Prantl & Růžicka, 1960 [= Phestiinae Logan, 1967; = ?Veteranellinae Chen, Liu & Lan, 1983]

Family SILICULIDAE Allen & Sanders, 1973⁶ [= Radiidentidae Egorova & Starobogatov, 1975]

Family TINDARIIDAE Verrill & Bush, 1897

Family YOLDIIDAE DALL, 1908

SF YOLDIINAE Dall, 1908

SF YOLDIELLINAE Allen & Hannah, 1986

⁴ Raised to family level by La Perna (2008).⁵ Malletiidae is in prevailing use and is conserved under ICZN Art. 40.2; see Nomenclator.⁶ Depending on the valid type species of *Silicula*, Siliculidae is either an objective synonym of Phaseoliidae or a potentially valid name with Radiidentidae as an objective synonym; see Nomenclator. We here treat it as a valid name, pending an application to the ICZN to solve the issue.² Following Ockelmann & Warén (1998).³ Nuculanidae is in prevailing use and is conserved under ICZN Art. 40.2; see Nomenclator.

Subclass Autobranchia Grobben, 1894**Superorder, Order, and SPF uncertain**

†Family CERCOMYIDAE Crickmay, 1936

?†PALAEOCARDIIDAE Scarlato & Starobogatov, 1979⁷†Family PUCAMYIDAE Sánchez in Sánchez & Benedetto, 2007⁸†**Superorder Nepiomorphia Kříž, 2007⁹**†**Order Praecardiida Newell, 1965**†**SPF PRAECARDIOIDEA R. Hoernes, 1884**

†Family PRAECARDIIDAE R. Hoernes, 1884 [= ? Pleurodontinae Conrath, 1887, inv. = Pararcidae Ulrich, 1894; = Neklaniidae Scarlato & Starobogatov, 1979]

†Family BUCHIOLIDAE Grimm, 1998

†**SPF CARDIOLOIDEA R. Hoernes, 1884**

†Family CARDIOLIDAE R. Hoernes, 1884

†Family SLAVIDAE Kříž, 1982

†**Order Antipleurida Kříž, 2007**†**SPF DUALINOIDEA Conrath, 1887**†Family DUALINIDAE Conrath, 1887 [= Antipleurinae Conrath, 1887¹⁰; = Praelucinidae Conrath, 1887¹¹; = Silurinidae Neumayr, 1891; = ?Dexiobiinae Newell & LaRocque, 1969]

†Family SPANILIDAE Kříž, 2007

†Family STOLIDOTIDAE Starobogatov, 1977

Superorder Pteriomorphia Beurlen, 1944¹²**Order and SPF uncertain**

†Family ELIGMIDAE Gill, 1871

†Family EVYANIDAE Carter, D. C. Campbell & M. R. Campbell, 2000

†Family ISCHYRODONTIDAE Scarlato & Starobogatov, 1979¹³

†Family LIMATULINIDAE Waterhouse, 2001

†Family MATHERIIDAE Scarlato & Starobogatov, 1979

†Family MYODAKRYOTIDAE Tunnicliff, 1987

†Family PICHLERIIDAE Scarlato & Starobogatov, 1979

†Family RHOMBOPTERIIDAE Korobkov, 1960

†Family UMBURRIDAE Johnston, 1991

Order Mytilida Férussac, 1822†**SPF MODIOLOPSOIDEA P. Fischer, 1886¹⁴**

†Family MODIOLOPSIDAE P. Fischer, 1886 [= Goniophorinidae Sánchez, 2006]

†Family COLPOMYIDAE Pojeta & Gilbert-Tomlinson, 1977

†Family SAFFORDIIDAE Scarlato & Starobogatov, 1979 [= Modiolodontidae Fang & Morris, 1997]

SPF MYTILOIDEA Rafinesque, 1815

Family MYTILIDAE Rafinesque, 1815

SF MYTILINAE Rafinesque, 1815 [= Adulinae Scarlato & Starobogatov, 1979; = Brachidontinae Scarlato & Starobogatov, 1979; = Perninae Scarlato & Starobogatov, 1979]

⁷ Whether Palaeocardiidae is more closely related to Praecardiidae or Ambonychiidae is uncertain.⁸ Anterior and subumbonal hinge and ligament are unknown, so it is uncertain if it is pteriomorphian or heteroconchian.⁹ Composition after Kříž (2007 and pers. com.).¹⁰ Priority of Dualinidae over simultaneously established Antipleurinae determined by ICZN Art. 24.1.¹¹ Priority of Dualinidae over simultaneously established Praelucinidae determined by First Reviser action by Kříž, pers. com. herein.¹² Preliminary molecular data (Giribet & Wheeler, 2002) indicate an internal topology of (Mytiloida (Arcoida ((Pinoidea (Pterioidea + Ostreoidea)) (Pectinoidea (Anomioidea + Limoidea)))).¹³ The presence of an external, opisthodetic, nearly horizontal, duplivincular ligament is apparent in Upper Ordovician *Ischyrodonta truncata* Ulrich (Frey, 1998: pl. 2, figs. 2, 3, 5).¹⁴ Superfamily composition following Fang and Morris (1997: 52).

(invalid); = Crenomytilini Kafanov, 1984; = Xenomytilinae Squires & Saul, 2006]¹⁵

SF BATHYMODIOLINAE Kenk & Wilson, 1985

SF CRENELLINAE Gray, 1840 [= Musculidae Iredale, 1939; = Arcuatulinae Scarlato & Starobogatov, 1979; = Trichomyinae Scarlato & Starobogatov, 1979]

SF DACRYDIINAE Ockelmann, 1983

SF LIMNOPERNINAE Scarlato & Starobogatov, 1979

SF LITHOPHAGINAE H. Adams & A. Adams, 1857 (1854) [= Lithodominae Gray, 1854]¹⁶; = Botulinae Scarlato & Starobogatov, 1979]

SF MODIOLINAE G. Termier & H. Termier, 1950 (*nomen protectum*) [= Jolyidae Bourguignat, 1880 (*nomen oblitum*)]

SF SEPTIFERINAE Scarlato & Starobogatov, 1979

†Family MYSIDIELLIDAE Cox, 1964

†**Order Cyrtodontida Scarlato & Starobogatov, 1971**

†**SPF CYRTODONTOIDEA Ulrich, 1894**

†Family CYRTODONTIDAE Ulrich, 1894

†Family PTYCHODESMATIDAE Scarlato & Starobogatov, 1984

†**SPF FALCATODONTOIDEA Cope, 1996**

†Family FALCATODONTIDAE Cope, 1996

Order Arcida Gray, 1854

SPF uncertain

†Family CATAMARCAIIDAE Cope, 2000

SPF ARCOIDEA Lamarck, 1809¹⁷

Family ARCIDAE Lamarck, 1809¹⁸

SF ARCINAE Lamarck, 1809 [= Thyasidae Gray,

¹⁵Adulinae belongs here, according to Ockelmann & Dinesen (2009).

¹⁶Lithophagiinae is in prevailing use and is conserved under ICZN Art. 40.2; see Nomenclator.

¹⁷Included extant families after Oliver & Holmes (2006).

¹⁸Division of this family into subfamilies is tentative. A ventral gape, hallmark of the Arcinae, is present in some genera placed in the Anadarinae. Molecular evidence is needed.

1857 (invalid); = Naviculidae MacNeil, 1937; = Litharcinae Frizzell, 1946; = Barbatidae Scarlato & Starobogatov, 1979; = Calloarcinae Scarlato & Starobogatov, 1979; = Porteriinae Scarlato & Starobogatov, 1979; = Hawaiarcinae Noda, 1986]

SF ANADARINAE Reinhart, 1935 [= Bathyarcidae Scarlato & Starobogatov, 1979; = Cunearcidae Scarlato & Starobogatov, 1979; = Lunarcidae Scarlato & Starobogatov, 1979; = Scaphulinae Scarlato & Starobogatov, 1979; = Seniliinae Scarlato & Starobogatov, 1979]

Family CUCULLAEIDAE Stewart, 1930 [= Idonearcidae Scarlato & Starobogatov, 1979; = Lopatiniidae Scarlato & Starobogatov, 1979]

†Family FREJIDAE Ratter & Cope, 1998

Family GLYCYMERIDIDAE Dall, 1908 (1847)

SF GLYCYMERIDINAE Dall, 1908 (1847) [= Pectunculidae Leach, 1847 (invalid); = Axinaeinae H. Adams & A. Adams, 1858; = Melaxinaeinae Habe, 1977; = Postligatidae Scarlato & Starobogatov, 1984]

†SF ARCULLAEINAE Newell, 1969

Family NOETIIDAE Stewart, 1930 [= Striarcinae MacNeil, 1937; = Trinacriinae MacNeil, 1937]¹⁹

†Family PARALLELODONTIDAE Dall, 1898

SF PARALLELODONTINAE Dall, 1898 [= Macrodontinae Meek & Hayden, 1865 (invalid); = Macrodonnellidae Scarlato & Starobogatov, 1979]

SF GRAMMATODONTINAE Stephenson, 1941²⁰ [= Nemodontinae Stephenson, 1941; = Cuculariinae Habe, 1977; = Catellidae Scarlato & Starobogatov, 1979; = Nordenskjöldiidae Scarlato & Starobogatov, 1979; = Obliquidontinae Astafieva-Urbajtis, 1994]

†**SPF GLYPTARCOIDEA Cope, 1996**

†Family GLYPTARCIDAE Cope, 1996

SPF LIMOPSOIDEA Dall, 1895²¹

Family LIMOPSIDAE Dall, 1895 [= ?Vasconellinae Scarlato & Starobogatov, 1979]

¹⁹Thomas et al. (2000) suggested that the supposedly unique ligamental pattern of the Noetiidae may, at least in part, represent a grade rather than a clade.

²⁰Priority over simultaneously established Nemodontinae determined by ICZN Art. 24.1.

²¹Included families after Oliver & Holmes (2006).

Family PHILOBRYIDAE F. Bernard, 1897 [= Hochstetteriidae Iredale, 1939 (n.a.); = Aupouriidae Scarlato & Starobogatov, 1979; = Limarcidae Scarlato & Starobogatov, 1979]

Order Pteriida Newell, 1965

†SPF AMBONYCHIOIDEA S. A. Miller, 1877²²

†Family AMBONYCHIIDAE S. A. Miller, 1877 [= Amphicoeliidae S. A. Miller, 1889; = Atomodesmatinae Waterhouse, 1976; = Malimaniniinae Waterhouse, 2001; = Permoceraminae Waterhouse, 2008]

?†Family ABIELLIDAE Starobogatov, 1970

†Family ALATOCONCHIDAE Termier, Termier & de Lapparent, 1974 [= Saikraconchinae Yancey & Ozaki, 1986]

†Family INOCERAMIDAE Giebel, 1852 [= Bathmoцерaminae Heinz, 1932 (n.a.); = Beloceraminae Heinz, 1932 (n.a.); = Boehmiceraminae Heinz, 1932 (n.a.); = Cinclidoceraminae Heinz, 1932 (n.a.); = Cladoceraminae Heinz, 1932 (n.a.); = Cordiceraminae Heinz, 1932 (n.a.); = Cremnoceraminae Heinz, 1932 (n.a.); = Cricoceraminae Heinz, 1932 (n.a.); = Cymatoceraminae Heinz, 1932 (n.a.); = Dactyloceraminae Heinz, 1932 (n.a.); = Epiceraminae Heinz, 1932 (n.a.); = Eugenoceraminae Heinz, 1932 (n.a.); = Gnesioceraminae Heinz, 1932 (n.a.); = Haenleiniiinae Heinz, 1932 (n.a.); = Helioceraminae Heinz, 1932 (n.a.); = Mytiloidinae Heinz, 1932; = Orthoceraminae Heinz, 1932 (n.a.); = Sphaeroceraminae Heinz, 1932 (n.a.); = Sphenoceramidae Heinz, 1932; = Stolleyiceraminae Heinz, 1932 (n.a.); = Tactoceraminae Heinz, 1932 (n.a.); = Tethyoceraminae Heinz, 1932 (n.a.); = Volviceraminae Heinz, 1932 (n.a.); = Taenioceraminae Aliev, 1958 (n.a.); = Anopaeinae Tsagareli & Gambashidze, 1984 (n.a.); = Neocomiceraminae Tsagareli & Gambashidze, 1984 (n.a.); = Sachalinoceraminae Zonova, 1984; = Coloniceramidae Pochialaynen, 1985 (n.a.)]

?†Family KINERKAELLIDAE Scarlato & Starobogatov, 1979

?†Family LUNULACARDIIDAE P. Fischer, 1887 [= Pterochaeniinae Fang & Ding, 1993; = Guangxiconchidae Zhang, 1999]

†Family MANTICULIDAE Waterhouse, 2008

†Family MONOPTERIIDAE Newell, 1969

†Family MYALINIDAE Frech, 1891 [= Selenimyaliniinae Weyer, 1968; = Kolymiidae Kuznetsov, 1973; = Naiaditidae Scarlato & Starobogatov, 1979; Anthraconautidae Kanev, 1980 (n.a.)]

?†Family PROKOPIEVSKIIDAE H. A. Vokes, 1967 [= Procopievskiidae Ragozin, 1933 (n.a.)]

†Family RAMONALINIDAE Yancey, M. A. Wilson & Mione, 2009

SPF PTERIOIDEA Gray, 1847 (1820)²³

Family PTERIIDAE Gray, 1847 (1820) [= Aviculidae Goldfuss, 1820²⁴; = Margaritidae Blainville, 1824; = Pterinellinae Hayami, 1965]

†Family BAKEVELLIIDAE King, 1850 [?= Dattidae Healey, 1908]

?†Family CASSIANELLIDAE Ichikawa, 1958 [= Paraviculidae Gugenberger, 1935 (n.a.)]

Family ISOGNOMONIDAE Woodring, 1925 (1828) [= Pernidae Fleming, 1828 (invalid); = Pernariinae Rafinesque, 1815; = Crenatulinae Gray, 1854; = Melininae Meek & Hayden, 1865; = Pedalionidae Stephenson, 1923]

?†Family KOCHIIDAE Frech, 1891

Family MALLEIDAE Lamarck, 1818 [= Vulsellidae Gray, 1854; = Reniellidae Iredale, 1939; = Stefaniniellidae Tavani, 1939]

†Family PERGAMIDIIDAE Cox, 1964
SF PERGAMIDIINAE Cox, 1964
SF ORETIINAE Waterhouse, 2008

†Family PLICATOSTYLIDAE Lupper & Packard, 1929 [= Lithiotidae Cox, 1971; = Cochlearitidae Benini & Loriga, 1977]

†Family POSIDONIIDAE Neumayr, 1891

†Family PTERINEIDAE Meek, 1864 [= Actinodesmatinae Maillieux, 1920; = Leiopteriinae Maillieux, 1920; = Actinopterellinae Maillieux, 1931; = Leptodesmatinae Maillieux, 1931; = Limopteriinae Maillieux, 1931; = Micropteriinae Maillieux, 1931; = Ahtioconchidae Eberzin, 1960]

²² Composition of Ambonychioidea presently under revision by JC.

²³ Family composition largely following Tëmkin (2006).

²⁴ Pteriidae is in prevailing usage and is conserved under ICZN Art. 40; see Nomenclator.

Family PULVINITIDAE Stephenson, 1941

†Family RETROCERAMIDAE Koschelkina, 1980

SPF PINNOIDEA Leach, 1819

Family PINNIDAE Leach, 1819

Order Ostreida Férussac, 1822

SPF OSTREOIDEA Rafinesque, 1815²⁵

Family OSTREIDAE Rafinesque, 1815

SF OSTREINAE Rafinesque, 1815

T OSTREINI Rafinesque, 1815 [= Tiostreidae Chanley & Dinamani, 1980]

T CRYPTOSTREINI Harry, 1985

T PUSTULOSTREINI Harry, 1985

T UNDULOSTREINI Harry, 1985

SF CRASSOSTREINAE Scarlato & Starobogatov, 1979

T CRASSOSTREINI Scarlato & Starobogatov, 1979

T STRIOSTREINI Harry, 1985

†T TURKOSTREINI Malchus, 1990

†SF FLEMINGOSTREINAE Stenzel, 1971

T FLEMINGOSTREINI Stenzel, 1971 [= ODONTOGYPHAEINI Vialov, 1983 (n.a.)]

T AMBIGOSTREINI Malchus, 1990

T CURVOSTREINI Malchus, 1990

T LIOSTREINI Vialov, 1983

SF LOPHINAE Vialov, 1936

T LOPHINI Vialov, 1936

T MYRAKEENINI Harry, 1985

†Family ARCTOSTREIDAE Vialov, 1983

SF ARCTOSTREINAE Vialov, 1983 [= Oscillophini Malchus, 1990]

SF PALAEOLOPHINAE Malchus, 1990

†Family CHONDRODONTIDAE Freneix, 1960 [= Lamellotidae Horvath, 1966]

Family GRYPHAEIDAE Vialov, 1936 [= Radiolaewellinae A. Ivanov, 1995²⁶]

†SF GRYPHAEINAE Vialov, 1936

†SF EXOGYRINAE Vialov, 1936 [= Amphidonteinae Vialov, 1983; = Ceratostreoninae Vialov, 1983; = Nanogyryni Malchus, 1990]

†SF GRYPHAEOSTREINAE Stenzel, 1971

SF PYCNODONTEINAE Stenzel, 1959

†T PYCNODONTINI Stenzel, 1959 [= Costeinae Vialov, 1983; = Monticulinidae A. Ivanov, 1995]

T HYOTISSINI Scarlato & Starobogatov, 1979

T NEOPYCNODONTINI Harry, 1985

Order Pectinida Gray, 1854

SPF uncertain:

†Family EUCHONDRIIDAE Newell, 1938²⁷

SF EUCHONDRIINAE Newell, 1938

SF CRENIPECTININAE Scarlato & Starobogatov, 1979

†Family PRAEOSTREIDAE Kříž, 1966

†Family PROSPONDYLIDAE Pchelintseva, 1960

†Family SAHAROPTERIIDAE G. Termier & H. Termier, 1972

†Family VLASTIDAE Neumayr, 1891

SPF ANOMIOIDEA Rafinesque, 1815

Family ANOMIIDAE Rafinesque, 1815 [= Heteranomiidae Scarlato & Starobogatov, 1979; = Placunopsidae Freneix, 1985]

†Family PERMANOMIIDAE Carter, 1990

Family PLACUNIDAE Rafinesque, 1815 [= Placentidae Gray, 1847; = Placunanomiinae Beu, 1967]

†SPF AULACOMYELLOIDEA ICHIKAWA, 1958²⁸

†Family AULACOMYELLIDAE Ichikawa, 1958

†Family BOSITRIDAE Waterhouse, 2008

†SPF AVICULOPECTINOIDEA Meek & Hayden, 1865²⁹

†Family AVICULOPECTINIDAE Meek & Hayden, 1865

SF AVICULOPECTININAE Meek & Hayden, 1865

SF ECHINIFERIPECTININAE Waterhouse, 2008

²⁵ Superfamily composition largely following Malchus (1990), with some modification by JC.

²⁶ Subfamiliar affiliation unknown.

²⁷ Family composition following Waterhouse (2008).

²⁸ Superfamily composition following Waterhouse (2008).

²⁹ Superfamily composition largely following Waterhouse (2008).

SF HAYASAKAPECTININAE Boyd & Newell, 2000
SF SPYRIDOPECTININAE Waterhouse, 2008
SF UNDOPECTININAE Waterhouse, 2001

†Family DELTOPECTINIDAE Dickins, 1957
SF DELTOPECTININAE Dickins, 1957
SF CYRTOROSTRINAE Newell & Boyd, 1995
SF SQUAMULIFERIPECTININAE Waterhouse, 2008

†SPF BUCHIOIDEA Cox, 1953 (1886)³⁰

†Family BUCHIIDAE Cox, 1953 (1886) [= Auce-
linae P. Fischer, 1886 (invalid)³¹]

†Family EURYDESMATIDAE Reed, 1932

†SPF CHAENOCARDIOIDEA S. A. Miller, 1889³²

†Family CHAENOCARDIIDAE S. A. Miller, 1889

†?Family BINIPECTINIDAE Feng & Liu, 1990

†Family STREBLOCHONDRIIDAE Newell, 1938
SF uncertain: Tribe FURCATIINI Waterhouse, 2001
SF STREBLOCHONDRIINAE Newell, 1938
SF GUIZHOUPECTININAE Astafieva, 1994
SF ORBICULOPECTININAE Waterhouse, 2001
T ORBICULOPECTININI Waterhouse, 2001
T EOCAMPTONECTINI Waterhouse, 2001
SF SATURNELLINAE Astafieva, 1994
SF STREBLOPTERIINAE Waterhouse, 2008

SPF DIMYOIDEA P. Fischer, 1886

Family DIMYIDAE P. Fischer, 1886 [= Atretidae
Scarlato & Starobogatov, 1979]

†SPF HETEROPECTINOIDEA Beurlen, 1954³³

†Family HETEROPECTINIDAE Beurlen, 1954
SF HETEROPECTININAE Beurlen, 1954

³⁰ Superfamily composition following Waterhouse (2008), except for present use of Buchioidea instead of Eurydesmatoidea.

³¹ Buchiidae is in prevailing usage and is conserved under ICZN Art. 40.2; see Nomenclator.

³² Superfamily composition following Waterhouse (2008), with slight emendation by JC.

³³ Superfamily composition largely following Waterhouse (2008), except that Heteropectinoidea is used instead of Etheripectinoidea, and Heteropectinidae is used instead of Etheripectinidae, based on family-group name priority.

SF ETHERIPECTININAE Waterhouse, 1982
SF CASSIANOIDINAE Newell & Boyd, 1995
SF GIRTYPECTININAE Waterhouse, 2008

†Family ACANTHOPECTINIDAE Newell & Boyd, 1995
SF ACANTHOPECTININAE Newell & Boyd, 1995
SF COSTATOPLICATININAE Waterhouse, 2008
SF LAMNIPECTININAE Waterhouse, 2008

†Family ANNULICONCHIDAE Astafieva, 1995

†Family LIMIPECTINIDAE Newell & Boyd, 1990

†SPF HALOBIOIDEA Kittl, 1912³⁴

†Family HALOBIIDAE Kittl, 1912

†Family CLARAIIDAE Gavrilova, 1996
SF CLARAIINAE Gavrilova, 1996
SF CHULUARIINAE Waterhouse, 2008
SF PSEUDOCALARAIINAE Gavrilova, 1996

†?Family DAONELLIDAE Neumayr, 1891

†SPF LEOPECTINOIDEA Krasilova, 1959³⁵

†Family LEOPECTINIDAE Krasilova, 1959

†SPF MONOTOIDEA P. Fischer, 1886³⁶

†Family MONOTIDAE P. Fischer, 1886

†Family DOLPONELLIDAE Waterhouse, 2001

†SPF OXYTOMOIDEA Ichikawa, 1958³⁷

†Family OXYTOMIDAE Ichikawa, 1958
SF OXYTOMINAE Ichikawa, 1958
SF MACCOYELLINAE Waterhouse, 2008

†Family OTAPIRIIDAE Waterhouse, 1982
SF OTAPIRIINAE Waterhouse, 1982

³⁴ Superfamily composition following Waterhouse (2008), except for tentative inclusion of Daonellidae. If the latter belongs here, the superfamily name would be based on Daonellidae rather than Halobiidae.

³⁵ Superfamily composition following Waterhouse (2008).

³⁶ Superfamily composition following Waterhouse (2008).

³⁷ Superfamily composition following Waterhouse (2008).

SF ASOELLINAE Begg & H. J. Campbell, 1986
SF AUCELLININAE Waterhouse, 2001

SPF PECTINOIDEA Rafinesque, 1815³⁸

Family PECTINIDAE Rafinesque, 1815

SF PECTININAE Rafinesque, 1815

T PECTININI Rafinesque, 1815 [= Amusiidae Ridewood, 1903; = Amussiopectinidae Glibert & van de Poel, 1965 (n.a.); = Eupectininae Teppner, 1922 (n.a.); = Fortipectininae Masuda, 1963; = Patinopectininae Habe, 1977; = Volinae Teppner, 1922]

T DECATOPECTININI Waller, 1986

†SF CAMPTONECTINAE Habe, 1977

SF CHLAMYDINAE Teppner, 1922 [= Subulachlamydiae Romanov, 1984 (n.a.); = Concentrichlamydiae Romanov, 1985 (n.a.); = Radulopectininae Romanov, 1985; Macrochlamydiae Kasum-Zade, 2003]

T CHLAMYDINI Teppner, 1922

T AUSTROCHLAMYDINI Jonkers, 2003

T CRASSADOMINI Waller, 1993

†SF MCLEARNIINAE Shurygin & Lutikov, 1991

SF PALLIOLINAE Korobkov, 1960 [= Pseudamussiinae F. Nordsieck, 1969; = Hemipectininae Habe, 1977]

T PALLIOLINI Korobkov, 1960

T ADAMUSSIINI Habe, 1977

†T EBURNEOPECTININI Waller, 2006

T MESOPEPLINI Waller, 2006

†T PSEUDENTOLIINI Waller, 2006

†T SERRIPECTININI Waller, 2006

SF PEDINAE Bronn, 1862 [= Aequipectinini F. Nordsieck, 1969; = Hinnitinae Habe, 1977; = Mimachlamyadini Waller, 1993]

†SF PSEUDOPECTININAE Kasum-Zade, 2003

†SF WEYLINAE Kasum-Zade, 2003

Family ENTOLIIDAE Teppner, 1922

†SF ENTOLIINAE Teppner, 1922

†SF PALAEOENTOLIINAE Romanov, 1985

SF SYNCYCLONEMATINAE Waller, 1978

†Family ENTOLIOIDESIDAE Kasum-Zade, 2003

†SF ENTOLIOIDESINAE Kasum-Zade, 2003

†SF CALVAENTOLIINAE Kasum-Zade, 2003

†Family NEITHEIDAE Sobetski, 1960

†Family PERNOPECTINIDAE Newell, 1938 [= Protoentoliinae Romanov, 1985]

Family PROPEAMUSSIIDAE Abbott, 1954

†Family TOSAPECTINIDAE Trushchelev, 1984

Family SPONDYLIDAE Gray, 1826 [= Dianchoridae Sobetski, 1977; = Spondylopectinidae Kasum-Zade & Romanov, 1987]

SPF PLICATULOIDEA Gray, 1854

Family PLICATULIDAE Gray, 1854

†SPF PSEUDOMONOTOIDEA Newell, 1938³⁹

†Family PSEUDOMONOTIDAE Newell, 1938

SF PSEUDOMONOTINAE Newell, 1938

SF PEGMAVALVULINAE Waterhouse, 2008

†Family HUNANOPECTINIDAE Yin, 1985

SF HUNANOPECTININAE Yin, 1985

SF LEPTOCHONDRIINAE Newell & Boyd, 1995

†Family TERQUEMIIDAE Cox, 1964

†SPF PTERINOPECTINOIDEA Newell, 1938⁴⁰

†Family PTERINOPECTINIDAE Newell, 1938

SF PTERINOPECTININAE Newell, 1938

SF PTERINOPECTINELLINAE Waterhouse, 2008

SF TESSERATIINAE Waterhouse, 2008

†Family NATALISSIMIDAE Waterhouse, 2008

SF NATALISSIMINAE Waterhouse, 2008

SF PSEUDAVICULOPECTININAE Waterhouse, 2008

Order Limida Moore, 1952

SPF LIMOIDEA Rafinesque, 1815

Family LIMIDAE Rafinesque, 1815

SF LIMINAE Rafinesque, 1815 [= Radulidae H. Adams & A. Adams, 1858; = Isolimeidae Kasum-Zade, 2003]

†SF CTENOSTREONINAE Kasum-Zade, 2003

SF LIMATULINAE Kasum-Zade, 2003 [= Calcaniculariini Waterhouse, 2008; = Echinorbinae Waterhouse, 2008]

†SF MYSIDIOPTERINAE Waterhouse, 2008

†SF PLAGIOSTOMINAE Kasum-Zade, 2003

³⁹Superfamily composition following Waterhouse (2008).

⁴⁰Superfamily composition following Waterhouse (2008).

³⁸Family-level content following Waller (2006b).

Superorder Heteroconchia Gray, 1854**Order uncertain:**

†Family AMNIGENIIDAE Khalfin, 1948

†Family LIPANELLIDAE Sánchez, 2005

† Family PALAEOMUTELIDAE Lahusen, 1897

Clade Palaeoheterodonta Newell, 1965⁴¹**Order Trigoniida Dall, 1889⁴²**†**SPF BEICHUANIOIDEA Liu & Gu, 1988**

†Family BEICHUANIIDAE Liu & Gu, 1988

†**SPF MEGATRIGONIOIDEA van Hoepen, 1929**

†Family MEGATRIGONIIDAE van Hoepen, 1929⁴³
 SF MEGATRIGONIINAE van Hoepen, 1929 [= Anditrigoniidae H. A. Leanza, 1993]
 SF APIOTRIGONIINAE Tashiro, 1979
 T APIOTRIGONIINI Tashiro, 1979
 T HETEROTRIGONIINI M. R. Cooper, 1991
 SF PTEROTRIGONIINAE van Hoepen, 1929 [= Scabrotrigoniini M. R. Cooper, 1989; = Linotrigoniinae Yanin, 2004]

†Family IOTRIGONIIDAE Saveliev, 1958

†Family RUTITRIGONIIDAE van Hoepen, 1929

†**SPF MYOPHORELLOIDEA Kobayashi, 1954⁴⁴**

†Family MYOPHORELLIDAE Kobayashi, 1954
 SF MYOPHORELLINAE Kobayashi, 1954
 SF STEINMANELLINAE M. R. Cooper, 1991

†Family BUCHOTRIGONIIDAE H. A. Leanza, 1993
 SF BUCHOTRIGONIINAE H. A. Leanza, 1993
 SF SYROTRIGONIINAE Pérez & Reyes, 1997

†Family LAEVITRIGONIIDAE Saveliev, 1958
 SF LAEVITRIGONIINAE Saveliev, 1958
 SF FRENGUELIELLINAE Nakano, 1960

†Family VAUGONIIDAE Kobayashi, 1954
 SF VAUGONIINAE Kobayashi, 1954
 SF QUADRATOTRIGONIINAE Saveliev, 1958

SPF TRIGONIOIDEA Lamarck, 1819⁴⁵

Family TRIGONIIDAE Lamarck, 1819
 SF TRIGONIINAE Lamarck, 1819 [= Lyrodontinae Bronn, 1862; = Neotrigoniinae Kobayashi, 1954]
 †SF MINETRIGONIINAE Kobayashi, 1954
 †SF NOTOTRIGONIINAE Skwarko, 1963 [= Austrotrigoniinae Skwarko, 1968]
 †SF PLEUROTIGONIINAE van Hoepen, 1929
 †SF NEUQUENITRIGONIINAE H. A. Leanza, 1993
 †SF PSILOTRIGONIINAE C. Fleming, 1987

†Family EOSCHIZODIDAE Newell & Boyd, 1975 [= Curtonotidae Dall, 1895 (invalid)]

†Family GROEBERELLIDAE Pérez, Reyes & Damborenea, 1995

†Family MYOPHORIIDAE Bronn, 1849 [= ?Cytherodontidae S. A. Miller, 1877; = Costatoriidae Newell & Boyd, 1975; = Gruenewaldiidae M. R. Cooper, 1991]

†Family PROSOGYROTRIGONIIDAE Kobayashi, 1954
 SF PROSOGYROTRIGONIINAE Kobayashi, 1954
 SF PRAEGONIINAE C. Fleming, 1962

†Family SCAPHELLINIDAE Newell & Ciriacks, 1962

†Family SCHIZODIDAE Newell & Boyd, 1975
 SF SCHIZODINAE Newell & Boyd, 1975
 SF EOASTARTINAE Newell & Boyd, 1975⁴⁶

†Family SINODORIDAE Pojeta & Zhang, 1984⁴⁷⁴¹ Ordinal and superfamily compositions by JC.⁴² Ordinal and superfamily compositions by JC.⁴³ Superfamily composition from M. R. Cooper, 1991.⁴⁴ Superfamily composition from M. R. Cooper, 1991, with addition of Buchotrigoniidae from Pérez & Reyes, 1997.⁴⁵ Composition of this superfamily follows Gu (1998) and Guo (1998b), with slight emendation by JC.⁴⁶ Schizodidae has priority over Eoastartidae following First Reviser action by Boyd & Newell (1997: 6); see Nomenclator.⁴⁷ Following Johnston & Zhang (1998).

Order Unionida Gray, 1854⁴⁸**†?SPF Archanodontoidea Modell, 1957⁴⁹**

†Family ARCHANODONTIDAE Modell, 1957

SPF uncertain:

†Family DESERTELLIDAE Dechaseaux, 1947

†Family TRIGONODIDAE Modell, 1942 [= Pachycardiidae Cox, 1961]

†Family UTSCHAMIELLIDAE Kolesnikov, 1977

SPF ETHERIOIDEA Deshayes, 1832⁵⁰Family ETHERIIDAE Deshayes, 1832⁵¹ [= Mulleriidae Deshayes, 1832; = Pseudomulleriidae Starobogatov, 1970⁵²]

Family IRIDINIDAE Swainson, 1840

SF IRIDININAE Swainson, 1840 [= Mutelidae Gray, 1847; = Spathinae Bronn, 1862; = Pleiodontidae Rochebrune, 1904]

SF ASPATHARIINAE Modell, 1942⁵³ [= Spathopsinae Modell, 1942]Family MYCETOPODIDAE Gray, 1840⁵⁴

SF MYCETOPODINAE Gray, 1840

SF ANODONTITINAE Modell, 1942 [= Bartlettinae Modell, 1942⁵⁵; = Glabarinae Modell, 1942⁵⁶; = Acostaeidae Morrison, 1973]

SF LEILINAE Morretes, 1949

SF MONOCONDYLAEINAE Modell, 1942 [= Fossulini Bonetto, 1966]

SPF HYRIOIDEA Swainson, 1840Family HYRIIDAE Swainson, 1840⁵⁷

SF HYRIINAE Swainson, 1840 [= Prisodontinae Modell, 1942]

T HYRIINI Swainson, 1840

T HYRIDELLINI McMichael & Hiscock, 1958 (1934) [= Propehyridellidae Iredale, 1934⁵⁸; = Cucumerunioninae Iredale, 1934]

T CASTALIINI Morretes, 1949

T DIPLODONTINI Ihering, 1901⁵⁹ [= Rhipidodontini Starobogatov, 1970]

SF VELESUNIONINAE Iredale, 1934 [= Lortellinae Modell, 1942]

†SPF TRIGONIOIDOIDEA Cox, 1952

†Family TRIGONIOIDIDAE Cox, 1952

SF TRIGONIOIDINAE Cox, 1952

⁴⁸The compromise classification presented herein is a result of combining proposed, and in some places conflicting, classifications by A. E. Bogan, D. Campbell, J. Hartman & W. R. Hoeh (pers. com.) and Graf & Cummings (2006). See also Campbell et al. (2005), Graf (2002), Hoeh et al. (2009) and Graf & Cummings (2010).

⁴⁹Placement of this superfamily in Order Unionida is uncertain.

⁵⁰Mulleriidae Deshayes, 1832, is the oldest name in this group and this priority issue needs addressing. See also notes for Etheriidae and Mycetopodidae.

⁵¹Graf & Cummings (2006) – see also reanalysis by Hoeh et al. (2009) and Graf & Cummings (2010) – included *Etheria*, *Acostaea*, and *Pseudomulleria* in Etheriidae. If *Acostaea* [= *Mulleria*] and *Etheria* belong to the same family, Mulleriidae has priority over simultaneously published Etheriidae following First Reviser action of Gill (1871: 20); see Nomenclator.

⁵²Placed here by Graf & Cummings (2006), but belonging to Unionidae following Bogan & Hoeh (2000) and Hoeh et al. (2009).

⁵³Aspathariinae has priority over Spathopsinae following First Reviser action by Graf & Cummings (2006: 394); see Nomenclator.

⁵⁴Bogan & Hoeh's (2000) molecular analyses placed *Etheria* close to *Acostaea* with the Mycetopodidae, while *Pseudomulleria* was placed in the Unionidae. If *Acostaea* [= *Mulleria*] and Mycetopoda belong to the same family, Mulleriidae has priority over Mycetopodidae (and, if placed there, over subfamily Anodontitinae).

⁵⁵Parodiz & Bonetto (1963: 190, 206) placed in Mycetopodidae and apparently advocated recognizing Bartlettinae over Anodontitinae and Glabarinae if the three prove synonymous. Starobogatov (1970) implicitly treated Bartlettinae as a synonym of Anodontitinae.

⁵⁶Priority of Anodontitinae over simultaneously published Glabarinae determined by First Reviser action by Parodiz & Bonetto (1963: 206).

⁵⁷Following Graf & Cummings (2006) revised classification based on molecular and morphological data. Questioned by Hoeh et al. (2009). Bogan, D. Campbell, Hartman & Hoeh (pers. com.) suggested subfamily rank for the listed tribes.

⁵⁸Priority over simultaneously established Cucumerunioninae determined by ICZN Art. 24.1.

⁵⁹Diplodontidae Ihering, 1901, is a homonym of Diplodontidae P. P. Carpenter, 1861. This case will require Commission ruling following ICZN Art. 55.3.1; see Nomenclator.

SF AMERICUNIONINAE Guo, 1986
 SF DANLENGICONCHINAE Sha, 1993
 SF MARTINSONELLINAE Sha, 1993
 SF PEREGRINOCONCHINAE Gu, Chen & Lan, 1976

†?Family JILINOCONCHIDAE Ma, 1989

†Family NAKAMURANAIADIDAE Guo, 1981 [= Sinonaiinae Chen, 1987; = Nippononaiidae Chen, 1988]

†Family PLICATOUNIONIDAE Chen, 1988

†Family PSEUDOHYRIIDAE Kobayashi, 1968

†Family SAINSCHANDIIDAE Kolesnikov, 1977

SPF UNIONOIDEA Rafinesque, 1820⁶⁰

Family UNIONIDAE Rafinesque, 1820

SF UNIONINAE Rafinesque, 1820

T UNIONINI Rafinesque, 1820 [= Cafferinae Modell, 1942; = Heudeaninae Modell, 1942; = Cuneopsinae Mongin, 1963 (n.a.); = Acuticostinae Starobogatov, 1967; = Nodulariinae Starobogatov & Zatravkin, 1987]

T ANODONTINI Rafinesque, 1820 [= Alasmidontinae Rafinesque, 1820; = Strophitinae Starobogatov, 1970; = Pseudanodontinae Stadnichenko, 1984; = Brachyanodontini Bogatov, Sayenko & Starobogatov, 2002 (n.a.)]

SF GONIDEINAE Ortmann, 1916⁶¹ [= Pseudodontinae Frierson, 1927⁶²; = Limnoscapinae Lindholm, 1932⁶³; = Hyriopsinae Modell, 1942; = Lamprotulinae Modell, 1942; = Leguminaiini Starobogatov, 1970; = Physunionini Starobogatov, 1970⁶⁴; = Psilunioninae Starobogatov, 1970]

SF AMBLEMINE Rafinesque, 1820

T AMBLEMINE Rafinesque, 1820

T LAMPSILINI Ihering, 1901 [= Propterinae Hannibal, 1912; = Cyprogeniinae Starobogatov, 1970; = Dromini Starobogatov, 1970; = Friersoniinae Starobogatov, 1970; = Glebulini Starobogatov, 1970; = Medionidinae Starobogatov, 1970; = Popenaiadinae Heard & Guckert, 1970; = Ptychobranchinae Starobogatov, 1970]

?T OXYNAIINI Starobogatov, 1970

T PLEUROBEMINI Hannibal, 1912 [= Elliptioninae Modell, 1942]

T QUADRULINI Ihering, 1901 [= Megalonaia-dinae Heard & Guckert, 1970⁶⁵]

SF COELATURINAE Modell, 1942⁶⁶ [= Pseudaviculinae Modell, 1942 (invalid); = Brazzaeinae Leloup, 1950; = Pseudospathinae Leloup, 1950 (n.a.); = Dentaspathariinae Modell, 1964; = Mweruellinae Pain & F. R. Woodward, 1968; = Prisodontopsinae Pain & F. R. Woodward, 1968]

SF MODELLNAIINAE Brandt, 1974

SF PARREYSIINAE Henderson, 1935⁶⁷ [= Diplasminae Modell, 1942; = Lamellidentinae Modell, 1942; = Arcidopsinae Starobogatov, 1970; = Hemisolasminae Starobogatov, 1970]

†SF QIYANGIIDAE Chen, 1983

SF RECTIDENTINAE Modell, 1942 [= Contradentinae Modell, 1942; = Nannonaiinae Modell, 1942⁶⁸]

?†Family LIAONINGIIDAE Yu & Dong, 1993 (invalid)⁶⁹

Family MARGARITIFERIDAE Henderson, 1929 (1910) [= Margaritaninae Ortmann, 1910; = Cumberlandiinae Heard & Guckert, 1970; = ?Promargaritiferidae F. R. Woodward, 1994 (n.a.)]

†Family SANCTICAROLITIDAE Simone & Mezzalira, 1997

⁶⁰ Unioninae has priority over Anodontinae following First Reviser action of Morrison (1956); see Nomenclator.

⁶¹ Alternatively placed as tribe Gonideini within Amblemiinae, by Graf & Cummings (2006).

⁶² Alternatively placed as SF *incertae sedis* with Leguminaiini in synonymy, by Graf & Cummings (2006).

⁶³ Alternatively placed as SF *incertae sedis* with Hyriopsinae in synonymy, by Graf & Cummings (2006).

⁶⁴ Alternatively placed as SF *incertae sedis*, by Graf & Cummings (2006).

⁶⁵ Following Graf & Cummings (2006).

⁶⁶ Starobogatov (1970) implicitly treated Dentaspathariinae as a synonym of Pseudospathinae Leloup, 1950, which is also in the coelaturine category. He put *Contradens* in Coelaturini but recognized Rectidentinae and Nannonaiini (the latter in Coelaturinae) and so did not establish priority of those three relative to each other.

⁶⁷ Also including Pseudomulleriidae Starobogatov, 1970 according to Hoeh et al. (2009) and Bogan, D. Campbell, Hartman & Hoeh (pers. com.).

⁶⁸ Nannonaiinae was placed *incertae sedis* within Unionidae by Graf & Cummings (2006).

⁶⁹ Name-bearing genus a junior homonym; see Nomenclator.

Clade Heterodonta Neumayr, 1884⁷⁰**Order and superfamily uncertain**

†Family ANODONTOPSIDAE S. A. Miller, 1889 [= Allodesmatidae Dall, 1895]

†Family BAIDIOSTRACIDAE Fang & Cope, 2008

†Family CARYDIIDAE Haffer, 1959

†Family INTIHUARELLIDAE Sánchez, 2003

†Family LYRODESMATIDAE P. Fischer, 1886

†Family MONTANARIIDAE Scarlato & Starobogatov, 1979

†Family NYASSIDAE S. A. Miller, 1877

†Family PSEUDARCIDAE Scarlato & Starobogatov, 1979

†Family REDONIIDAE Babin, 1966

†Family TANAODONTIDAE Liu, 1976

†Family ZADIMERODIIDAE Guo, 1988

Order Lucinida Gray, 1854**†SPF BABINKOIDEA Horný, 1960**

†Family BABINKIDAE Horný, 1960

†Family COXICONCHIIDAE Babin, 1977

SPF LUCINOIDEA J. Fleming, 1828⁷¹

Family LUCINIDAE J. Fleming, 1828⁷²

SF LUCININAE J. Fleming, 1828 [= Divaricellidae Korobkov, 1954]

SF CODAKIINAE Korobkov, 1954

SF FIMBRIINAE Nicol, 1950 (1870) [= Corbinae Stoliczka, 1870]

†SF ILIONIINAE Scarlato & Starobogatov, 1979

SF MILTHINAE Chavan, 1969

SF MYRTEINAE Chavan, 1969

†Family MACTROMYIDAE Cox, 1929 (1887) [= Unicardiidae P. Fischer, 1887]

†Family PARACYCLIDAE Johnston, 1993

SPF THYASIROIDEA Dall, 1900 (1895)⁷³

Family THYASIRIDAE Dall, 1900 (1895) [= Cryptodontidae Dall, 1895⁷⁴; = Axinopsidinae F. R. Bernard, 1983]

†Order Actinodontida Dechaseaux, 1952**†SPF CYCLOCONCHOIDEA Ulrich, 1894**

†Family CYCLOCONCHIDAE Ulrich, 1894

SF CYCLOCONCHINAE Ulrich, 1894

SF TASELASMODINAE Fang & Cope, 2008

†Family ACTINODONTIDAE Davies, 1933⁷⁵

Order Carditida Dall, 1889⁷⁶**SPF uncertain**

†Family AENIGMOCONCHIDAE Betekhtina, 1968

†Family PALAEOCARDITIDAE Chavan, 1969 [= Septocardiidae Kafanov & Starobogatov, 1977]

Family CARDINIIDAE Zittel, 1881⁷⁷

†Family MYOPHORICARDIIDAE Cox & Chavan, 1969 [= Myophoriopidae Chavan, 1969 (n.a.)]

⁷³ Molecular data (e.g., Taylor et al., 2009) place this as independent clade removed from Lucinoidea.

⁷⁴ Thyasiridae is conserved under ICZN Art. 40.2; see Nomenclator.

⁷⁵ The name Actinodontidae is used here provisionally, pending a decision of the Commission on its homonymy with Actinodontidae Lydekker, 1885 (see Nomenclator).

⁷⁶ Molecular data (Giribet & Distel, 2003) suggest that this group is outside of and sister to the Euheterodonta, the latter including Lucinoidea.

⁷⁷ This family, otherwise extinct since the Mesozoic, has been reported as living with a single genus and species, the Panamic *Tellidorella cristulata* S. S. Berry, 1963 (Cox & Chavan, in Moore, 1969: 580). This hypothesis should be a high priority for molecular study.

⁷⁰ Recent molecular data, e.g., Taylor et al. (2009), do not support the orders as given below.

⁷¹ With Lucinidae as only extant representative, following Taylor & Glover (2006).

⁷² The current breakdown in previously named subfamilies is not fully supported by forthcoming molecular studies (J. D. Taylor, pers. com.).

SPF CARDITOIDEA Férussac, 1822

Family CARDITIDAE Férussac, 1822⁷⁸

SF CARDITINAE Férussac, 1822

SF CARDITAMERINAE Chavan, 1969

SF CARDITESINAE Chavan, 1969

SF MIODOMERIDINAE Chavan, 1969

SF THECALIINAE Dall, 1903

SF VENERICARDIINAE Chavan, 1969

Family CONDYLOCARDIIDAE F. Bernard, 1896

SF CONDYLOCARDIINAE F. Bernard, 1896 [= Benthocardiellidae Iredale & McMichael, 1962 (n.a.)]

?SF CARDITELLINAE Kuroda, Habe & Oyama, 1971

SF CUNINAE Chavan, 1969

SPF CRASSATELLOIDEA Férussac, 1822

Family CRASSATELLIDAE Férussac, 1822

SF CRASSATELLINAE Férussac, 1822 [= Crassatellitidae Dall, 1895 (n.a.); = Eucrassatellitidae Iredale & McMichael, 1962 (n.a.)]

SF SCAMBULINAE Chavan, 1952

†SF ORIOCRASSATELLINAE Boyd & Newell, 1968

Family ASTARTIDAE d'Orbigny, 1844 (1840) [= Prosocoelidae Karczewski, 1992⁷⁹]

SF ASTARTINAE d'Orbigny, 1844 (1840) [= Crassinidae Gray, 1840⁸⁰]

†SF HOLDHAUSIELLINAE Beurlen, 1954 [= Terraidae Scarlato & Starobogatov, 1979]

†SF ASTARTELLINAE Boyd & Newell, 1968

†SF ERIPHYLINAE Chavan, 1952

†SF OPINAE Chavan, 1952

†SF PINZONELLINAE Beurlen, 1954

†SF TRIGONOPINAE R. N. Gardner & H. J. Campbell, 2002

†Family EODONIDAE Carter, D. C. Campbell & M. R. Campbell, 2000

†Family PTYCHOMYIDAE Keen, 1969

⁷⁸As noted by Morris (1978: 273), the subfamilial classification of this family is particularly suspect, being based on overlapping shape, sculptural, and hinge details. This family is a prime candidate for modern reevaluation using anatomical and molecular evidence.

⁷⁹Placement in subfamily and family uncertain; genus *Prosocoelus* placed in Astartellinae by Boyd & Newell (1968), and in Opinae by Chavan (in Moore, 1969: 572).

⁸⁰Astartidae is in prevailing usage and is conserved under ICZN Art. 40.2; see Nomenclator.

Order uncertain

†**SPF ANTHRACOSIOIDEA Amalitsky, 1892**⁸¹

†Family ANTHRACOSIIDAE Amalitsky, 1892

†Family CARBONICOLIDAE Cox, 1932

SF CARBONICOLINAE Cox, 1932

SF OLIGODONTELLINAE Starobogatov, 1987

SF PALAEANODONTINAE Modell, 1964

?†Family OPOKIELLIDAE Kanev, 1983

†Family PRILUKIELLIDAE Starobogatov, 1970

SF PRILUKIELLINAE Starobogatov, 1970

SF SENDERZONIELLINAE Betekhtina, Starobogatov & Jatsuk, 1987 [= Microdontidae Weir, 1969 (invalid); = Microdontellidae Gusev, 1969 (invalid)]

†Family SHAANXICONCHIDAE Liu, 1980

†Family SINOMYIDAE Scarlato & Starobogatov, 1979

†**“Megalodonts”**⁸²

†Family CONGERIOMORPHIDAE Saul, 1976

†Family DICEROCARDIIDAE Kutassy, 1934

†Family MECYNODONTIDAE Haffer, 1959

†Family MEGALODONTIDAE Morris & Lycett, 1853

†Family PACHYRISMATIDAE Scarlato & Starobogatov, 1979 (= Megalodidae Karczewski, 1992, inv.)

†Family PLETHOCARDIIDAE Scarlato & Starobogatov, 1979

†Family WALLOWACONCHIDAE Yancey & Stanley, 1999

⁸¹Placement of Anthracosioidea in order Unionoida follows Weir (1969: N404), but needs further examination.

⁸²An informal and in part poorly known group of “megalodont” families, considered distinct from the rudists (following Skelton, pers. com., 1 February 2010).

†**Order Hippuritida Newell, 1965**^{83,84}

†**SPF RADIOLITOIDEA d'Orbigny, 1847**⁸⁵

†Family RADIOLITIDAE d'Orbigny, 1847 [= Sphaerulitidés Douvillé, 1886 (n.a.); = Lapeirousiinae Kühn, 1932; = Sauvagesiidae Wiontzek, 1934; = Biradiolitinae Dechaseaux & Coogan, 1969; = Chiapasellidae Alencaster, 1971; = Joufiinae Karacabey-Oztemür, 1981; = Pseudopolyconitidae Sladic-Trifunovic, 1983; = Duraniidae Yanin, 1990; = Osculigeridae Yanin, 1990]

†Family ANTILLOCAPRINIDAE MacGillavry, 1937

†Family CAPRINIDAE d'Orbigny, 1847
SF CAPRININAE d'Orbigny, 1847
SF CAPRINULOIDEINAE Damestoy, 1971 [= Coalcomaninae Coogan, 1973; = Rethidae Yanin, 1990]

†Family CAPRINULIDAE Yanin, 1990

†Family CAPROTINIDAE Gray, 1848 [= ?Heterocaprinidae Munier-Chalmas, 1873; = Gyropleuridae MacGillavry, 1935; = Polyconitinae MacGillavry, 1937; = Horiopleuridae Yanin, 1990]

†Family DICERATIDAE Dall, 1895

†Family HIPPURITIDAE Gray, 1848 [= Barrettiinae Chubb, 1971; = Torreitinae Grubic, 1979; = Hippuritellinae Bilotte, 1982; = Pseudovacinitinae Bilotte, 1982; = Batolitidae Yanin, 1990⁸⁶; = Pironaeidae Yanin, 1990]

†Family ICHTHYOSARCOLITIDAE Douvillé, 1887 (1871) [= Caprinellidae Gill, 1871⁸⁷]

†Family MONOPLEURIDAE Munier-Chalmas, 1873

†Family PLAGIOPTYCHIDAE Douvillé, 1888

†Family TRECHMANELLIDAE Cox, 1934 [= Anomoptychidae H. A. Vokes, 1967; = Dictyoptychidae Skelton, 1993]

†**SPF REQUIENIOIDEA Kutassy, 1934**

†Family REQUIENIIDAE Kutassy, 1934 [= Bayleidae Munier-Chalmas, 1873 (*nomen oblitum*); = Toucasiidae Pchelintsev, 1959 (n.a.)]

†Family EPIDICERATIDAE Rengarten, 1950 [= Heterodiceratidae Pchelintsev, 1959; = Pleiodiceratinae Pchelintsev, 1959]

Order Venerida Gray, 1854

SPF uncertain

Family HEMIDONACIDAE Scarlato & Starobogatov, 1971⁸⁸

SPF ARCTICOIDEA Newton, 1891 (1844)

Family ARCTICIDAE Newton, 1891 (1844) [= Cyprinidae d'Orbigny, 1844⁸⁹; = Cyprinidaeidae Rovereto, 1900]

†Family EULOXIDAE J. Gardner, 1943

†Family ISOCYPRINIDAE R. N. Gardner, 2005

†Family POLLICIDAE Stephenson, 1953

Family TRAPEZIDAE Lamy, 1920 (1895) [= Cypricardiidae Dall, 1895⁹⁰; = Libitinidae Thiele, 1926; = Lithophagellidae Cossmann, 1911 (n.a.); = Kitsoniidae Eames, 1957]

†Family VENIELLIDAE Dall, 1895 [= Veniliidae Meek, 1864 (invalid)]

⁸³Classification based on document prepared by Peter Skelton (pers. com.) for the rudist part of the Treatise on Invertebrate Paleontology, with nomenclatural adjustments herein.

⁸⁴The name Rousseliinae MacGillavry, 1937, is not yet placed.

⁸⁵Priority over simultaneously established Caprinidae determined by First Reviser action of Bouchet & Rocroi, see Nomenclator.

⁸⁶The name Batolitidae Yanin, 1990 has been added to the synonymy of Hippuritidae based on <http://www.paleotax.de/rudists/>.

⁸⁷Ichthyosarcolitidae is conserved under ICZN Art. 40.2; see Nomenclator.

⁸⁸Position uncertain; following Healy et al. (2008).

⁸⁹Arcticidae is in prevailing usage and is conserved under ICZN Art. 40.2; see Nomenclator.

⁹⁰Trapezidae is in prevailing usage and is conserved under ICZN Art. 40.2; see Nomenclator.

SPF CARDIOIDEA Lamarck, 1809⁹¹

Family CARDIIDAE Lamarck, 1809⁹² [= Pterocardiidae Scarlato & Starobogatov, 1979⁹³]

SF CARDIINAE Lamarck, 1809 [= Dinocardiini Kafanov, 1977; = Acanthocardiini Kafanov & Starobogatov, 1977; = Vepricardiini Kafanov & Starobogatov, 1977]

SF CLINOCARDIINAE Kafanov, 1975 [= Serripedini Kafanov, 1975; = Profulviini Kafanov & Popov, 1977]

SF FRAGINAE Stewart, 1930 [= Parvicardiini Kafanov & Starobogatov, 1977; = Goniocardiidae Scarlato & Starobogatov, 1979]

†SF LAHILLIINAE Finlay & Marwick, 1937

SF LAEVICARDIINAE Keen, 1951 [= Nemocardiinae Savazzi, 1985]

SF LYMNOCARDIINAE Stoliczka, 1870⁹⁴

T LYMNOCARDIINI Stoliczka, 1870

†ST LYMNOCARDIINA Stoliczka, 1870

ST CERASTODERMATINA F. Nordsieck, 1969

†ST ACOBAECARDIINA Paramonova, 1986

†ST AVICULOCARDIINA Paramonova, 2001

†ST CHARTOCONCHINA Taktakishvili, 1987

†ST CHOKRAKIINA Popov, 2001

†ST DIGRESSODACNINA Taktakishvili, 1987

†ST MERKLINICARDIINA Popov, 2001

†ST OBSOLETIFORMINA Paramonova, 2001

†ST PACHYDACNINA Andreescu, 1975

†ST PANTICAPAEINA Taktakishvili, 1987

†ST PHYLLOCARDIINA Nevesskaya, 1986

†ST PLANACARDIINA Paramonova, 2001

†ST PLICATIFORMINA Paramonova, 2001

†ST PONTALMYRINA Taktakishvili, 1987

†ST PRIONOPLEURINA Taktakishvili, 1987

†ST PSEUDOCATILLINA Taktakishvili, 1987

T ADACNINI Gill, 1871 [= Hypaninae Starobogatov, 1970; = Avicardiini Popov, 1977; = Hyrcaniini Kafanov & Starobogatov, 1977 (invalid)]

†T DIDACININI Eberzin, 1962

†T LIMNOPAPPIINI Schlickum, 1962

†T PARADACNINI Eberzin, 1967 [= Arcicardiini Nevesskaya, 1986]

†T PROSODACNINI Keen, 1937 [= Psilodontini Taktakishvili, 1987 (invalid); = Stylodacninae Papaianopol, 1987]

†T PSEUDOCARDITINI Keen, 1969

†?T TRAPEZICARDIINI Kanjilal & Srinivasan, 2002

†SF PLEURIOCARDIINAE Schneider, 1995

SF ORTHOCARDIINAE Schneider, 2002

†SF PROFRAGINAE Badve, 1977

SF PROTOCOLIINAE Reuss, 1846

SF TRACHYCARDIINAE Stewart, 1930

SF TRIDACNINAE Lamarck, 1819 [= Chametracheidae H. Adams & A. Adams, 1857; = Aviculariidae Scarlato & Starobogatov, 1979]

†SF TULONGOCARDIINAE Schneider, 1995

SPF CHAMOIDEA Lamarck, 1809

Family CHAMIDAE Lamarck, 1809 [= Arcinellidae Scarlato & Starobogatov, 1971]

SPF CYAMIOIDEA G. O. Sars, 1878⁹⁵

Family CYAMIIDAE G. O. Sars, 1878 [= Perrierinidae Marwick, 1928; = Cyamiomactridae Iredale & McMichael, 1962 (n.a.)]

Family BASTEROTIIDAE Cossmann, 1909 [= Eucharidae Récluz, 1869 (invalid)]

Family GALATHEAVALVIDAE Knudsen, 1970

Family SPORTELLIDAE Dall, 1899

SPF CYRENOIDEA Gray, 1840

Family CYRENIDAE Gray, 1840 [= Corbiculidae Gray, 1847⁹⁶; = Serrilaminulinae Lindholm, 1933; = Geloinidae Iredale, 1943; = Polymesodinae Habe, 1977]

?Family GLAUCONOMIDAE Gray, 1853 [= Glaucomyidae P. P. Carpenter, 1861]⁹⁷

⁹¹ Classification of Cardioidea largely from Schneider (1992, 1995, 1998a, 1998b, 2002), with additions by JC and GC.

⁹² Some authors have recognized the Lymnocardiidae and Tridacnidae as separate families, but this would result in paraphyly (Schneider, 1995, 1998, 2002; Schneider & Carter, 2001; Kirkendale, 2009).

⁹³ Subfamiliar affiliation uncertain.

⁹⁴ Paleontologists have divided the Lymnocardiinae into a myriad of named units – here charitably listed as tribes and subtribes.

⁹⁵ The composition of this superfamily, whose members mostly have external ligaments, and its relationship to the Galeommatoidea (mostly with internal ligaments), are not yet resolved.

⁹⁶ The available senior name, Cyrenidae, has been in use and cannot be considered a *nomen oblitum*.

⁹⁷ Sperm characters do not support close relationship with Veneroidea, Cyrenoidea, Myoidea, Mactroidea, Tellinoidea, or Crassatelloidea (Healy et al., 2006). Molecular data by Taylor et al. (2009) place this with Cyrenoididae and Corbiculidae (now Cyrenidae).

SPF CYRENOIDOIDEA H. Adams & A. Adams, 1857 (1853)

Family CYRENOIDIDAE H. Adams & A. Adams, 1857 (1853) [= Cyrenellidae Gray, 1853⁹⁸]

SPF DREISSENOIDEA Gray, 1840

Family DREISSENIDAE Gray, 1840⁹⁹

SF DREISSENINAE Gray, 1840 [= Enocephaliidae de Stefani, 1880; = Tichogoniidae Andrusov, 1893]

SF DREISSENNOMYINAE Babak, 1983

SPF GAIMARDIOIDEA Hedley, 1916

Family GAIMARDIIDAE Hedley, 1916 [= Modiolaridae Gray, 1854]

SPF GALEOMMATOIDEA Gray, 1840

Family GALEOMMATIDAE Gray, 1840 [= Chlamydoconchinae Dall, 1884; = Solecardiidae Allan, 1950 (n.a.); = Marikelliidae Iredale & McMichael, 1962 (n.a.); = Scintillidae Iredale & McMichael, 1962 (n.a.); = ?Cyamionematiidae Scarlato & Starobogatov, 1979; = Ehippodontidae Scarlato & Starobogatov, 1979; = Vasconiellidae Scarlato & Starobogatov, 1979]¹⁰⁰

Family LASAEIDAE Gray, 1842 [= Leptonidae Gray, 1847; = Kelliidae Forbes & Hanley, 1849; = Erycinidae Deshayes, 1850 (invalid); = Montacutidae W. Clark, 1855; = Scacchiidae Récluz, 1869; = Borniolidae Iredale & McMichael, 1962 (n.a.); = Melliterycinae Iredale & McMichael, 1962 (n.a.); = Micropoliidae Iredale & McMichael, 1962 (n.a.); = Myllitidae Iredale & McMichael, 1962 (n.a.); = Borniinae F. R. Bernard, 1983; = Mysellinae F. R. Bernard, 1983; = Oorbitellinae F. R. Bernard, 1983; = Thecodontinae F. R. Bernard, 1983]¹⁰¹

SPF GLOSSOIDEA Gray, 1847 (1840)

Family GLOSSIDAE Gray, 1847 (1840) [= Isocardiidae Gray, 1840¹⁰²; = Bucardiidae H. Adams & A. Adams, 1857]

Family KELLIELLIDAE P. Fischer, 1887 [= Alveinidae Glibert & van de Poel, 1966 (n.a.); = Lutetiidae Zhgenti, 1976]

Family VESICOMYIDAE Dall & Simpson, 1901 [= Pliocardiidae Woodring, 1925]

SPF MACTROIDEA Lamarck, 1809

Family MACTRIDAE Lamarck, 1809

SF MACTRINAE Lamarck, 1809 [= Gnathodontidae Neumayr, 1884 (invalid); = Rangiidae P. Fischer, 1884]

SF LUTRARIINAE Gray, 1853

SF KYMATOXINAE Stenzel & Krause, 1957 [= Pteropsinae Dall, 1894 (invalid); = Pteropsellinae Keen, 1969]

SF TANYSIPHONINAE Scarlato & Starobogatov, 1971

SF ZENATIINAE Dall, 1895 [= Resaniinae Marwick, 1931]

Family ANATINELLIDAE Deshayes, 1853

Family CARDILIIDAE P. Fischer, 1887¹⁰³

Family MESODESMATIDAE Gray, 1840

SF MESODESMATINAE Gray, 1840 [= Paphiinae Gray, 1847 (invalid); = Myadesmatidae B. L. Clark, 1922; = Donacillidae MacPherson & Gabriel, 1962]

SF DAVILINAE Dall, 1895

SPF SPHAERIOIDEA Deshayes, 1855 (1820)

Family SPHAERIIDAE Deshayes, 1855 (1820)

SF SPHAERIINAE Deshayes, 1854 (1820) [= Cycladidae Rafinesque, 1820 (invalid); = Corneocycladidae Hannibal, 1912; = Sphaeriastrinae Alimov & Starobogatov, 1968; = Musculiinae Starobogatov, 1984]

⁹⁸ Cyrenoididae is in prevailing usage and is conserved under ICZN Art. 40.2; see Nomenclator.

⁹⁹ Following Nuttall (1990).

¹⁰⁰ There is as yet insufficient information to divide this family into supported clades.

¹⁰¹ There is as yet insufficient information to divide this family into supported clades.

¹⁰² Glossidae is in prevailing usage and is conserved under ICZN Art. 40.2; see Nomenclator.

¹⁰³ With shell morphology otherwise suggesting similarity to the Cardiidae, but an internal ligament, this family would be a prime candidate for molecular investigation.

SF EUGLESINAE Pirogov & Starobogatov, 1974
[= Neopisidiinae Korniushev, 1989]

SF EUPERINAE Heard, 1965

SF PISIDIINAE Gray, 1857 [= Lacustrininae Korniushev, 1989]

?†Family FERGANOCONCHIDAE Martinson, 1961

†Family KIJIDAE Kolesnikov, 1977

†Family LIMNOCYRENIDAE Kolesnikov, 1977

†?Family NEOMIODONTIDAE Casey, 1955 [= Eomiodontinae Hayami, 1965]

†Family PSEUDOCARDINIIDAE Martinson, 1961

†Family SIBIRECONCHIDAE Kolesnikov, 1977

SPF TELLINOIDEA Blainville, 1814

Family TELLINIDAE Blainville, 1814 [= Macominae Olsson, 1961; = Arcopagiinae Kuroda, Habe & Oyama, 1971 (n.a.); = Strigillinae Habe, 1977]

Family DONACIDAE J. Fleming, 1828

†Family ICANOTIIDAE Casey, 1961

Family PSAMMOBIIDAE J. Fleming, 1828 [= ?Azoriidae Leach, 1852¹⁰⁴; = Capsinae Stoliczka, 1870; = Garinae Stoliczka, 1870; = Asaphidae Winckworth, 1932¹⁰⁵; = Sanguinolariinae M. Smith, 1937]

Family SEMELIDAE Stoliczka, 1870 (1825)

SF SEMELINAE Stoliczka, 1870 (1825) [= Amphidesmatidae Latreille, 1825; = Cumingiinae Stoliczka, 1870]

SF ERVILIINAE Dall, 1895

SF SCROBICULARIINAE H. Adams & A. Adams, 1856 [= Lavignonidae Récluz, 1869]

Family SOLECURTIDAE d'Orbigny, 1846

†Family SOWERBYIDAE Cox, 1929 [= Isodontidae Arkell, 1934]

†Family TANCREDIIDAE Meek, 1864

†Family UNICARDIOPSIDAE Chavan, 1969

†Family QUENSTEDTIIDAE Cox, 1929

SPF UNGULINOIDEA Gray, 1854¹⁰⁶

Family UNGULINIDAE Gray, 1854 [= Diplodontidae Carpenter, 1861]

SPF VENEROIDEA Rafinesque, 1815¹⁰⁷

Family VENERIDAE Rafinesque, 1815

SF VENERINAE Rafinesque, 1815

SF CALLOCARDIINAE Dall, 1895 [= Pitarinae Stewart, 1930; = Callistinae Habe & Kosuge, 1967 (invalid)]

SF CHIONINAE Frizzell, 1936¹⁰⁸ [= Cyclininae Frizzell, 1936; = Mclellaniinae Wilson, 1983]

SF CLEMENTIINAE Frizzell, 1936

SF DOSINIINAE Deshayes, 1853 [= Arteminae Hutton, 1880]

SF GEMMINAE Dall, 1895

SF GOULDIINAE Stewart, 1930 [= Circinae Dall, 1895 (invalid); = Gafrariidae Korobkov, 1954]

SF LIOCONCHINAE Habe, 1977

SF MERETRICINAE Gray, 1847 (1838) [= Cythereinae Gray, 1838 (invalid)]

SF SAMARANGIINAE Keen, 1969

SF PETRICOLINAE d'Orbigny, 1840 [= Mysiidae Gray, 1854; = Cooperellidae Dall, 1900]

SF SUNETTINAE Stoliczka, 1870 [= Meroinae Tryon, 1884]

SF TAPETINAE Gray, 1851 [= Paphiinae Finlay, 1928 (invalid); = Oncophoridae Davitashvili, 1934 (invalid); = Rzehakiidae Korobkov, 1954]

SF TURTONIINAE W. Clark, 1855

Family NEOLEPTONIDAE Thiele, 1934 [= Bernardinidae Keen, 1969]

¹⁰⁴A synonym of Psammobiidae or of Solecurtidae. See Nomenclator.

¹⁰⁵Asaphidae is a junior homonym of Asaphidae Burmeister, 1843, which is in current use in the trilobites (see Nomenclator). Any use of the molluscan name (e.g., as a subfamily name) will require an application to the ICZN to have the name modified.

¹⁰⁶As recognized by Taylor et al. (2009).

¹⁰⁷For discussion of subfamilies see Mikkelsen et al. (2006).

¹⁰⁸Priority over simultaneously established Cyclininae determined by ICZN Art. 24.1.

Order Myida Stoliczka, 1870**SPF MYOIDEA Lamarck, 1809**

Family MYIDAE Lamarck, 1809

SF MYINAE Lamarck, 1809

SF CRYPTOMYINAE Habe, 1977

SF SPHENIINAE F. R. Bernard, 1983

Family CORBULIDAE Lamarck, 1818

SF CORBULINAE Lamarck, 1818 [= Aloididae Thiele, 1934; = Caryocorbulinae H. A. Vokes, 1945; = Potamocorbulinae Habe, 1977]

†SF CAESTOCORBULINAE H. A. Vokes, 1945

†SF CORBULAMELLINAE H. A. Vokes, 1945

SF LENTIDIINAE H. A. Vokes, 1945

†SF PACHYDONTINAE H. A. Vokes, 1945

Family ERODONIDAE Winckworth, 1932

†Family PLEURODESMATIDAE Cossmann, 1909

†Family RAETOMYIDAE Newton, 1919 [= Amotapidae Olsson, 1928]

SPF PHOLADOIDEA Lamarck, 1809

Family PHOLADIDAE Lamarck, 1809

SF PHOLADINAE Lamarck, 1809 [= Hypogaeidae Rafinesque, 1815; = Zirfaeinae Gray, 1851; = Euxinibarneini Zhgenti, 1991]

SF JOUANNETIINAE Tryon, 1862

SF MARTESIINAE Grant & Gale, 1931 [= Pholadideinae Taki & Habe, 1955 (n.a.); = Teredininae Tryon, 1862]

SF XYLOPHAGINAE Purchon, 1941¹⁰⁹

Family TEREDINIDAE Rafinesque, 1815

SF TEREDININAE Rafinesque, 1815 [= Zachsinae Habe, 1977]

SF BANKIINAE Turner, 1966

SF KUPHINAE Tryon, 1862 [= Furcellinae Bronn, 1862]

Order uncertain**SPF HIATELLOIDEA Gray, 1824**

Family HIATELLIDAE Gray, 1824 [= Saxicavidae

Swainson, 1835; = Glycimeridae Bronn, 1849 (invalid); = Pholeobiidae Leach, 1852; = Panopeinae Bronn, 1862; = Saxicavellinae Scott, 1994]

SPF SOLENOIDEA Lamarck, 1809¹¹⁰

Family SOLENIDAE Lamarck, 1809

Family PHARIDAE H. Adams & A. Adams, 1856¹¹¹

SF PHARINAE H. Adams & A. Adams, 1856

SF SILIQUINAE Bronn, 1862

SF PHARELLINAE Stoliczka, 1870

SF NOVACULININAE Ghosh, 1920

SF CULTELLINAE Davies, 1935

Order uncertain**†SPF MODIOMORPHOIDEA S. A. Miller, 1877¹¹²**

†Family MODIOMORPHIDAE S. A. Miller, 1877 [= Palanatinidae S. A. Miller, 1877; = Butovicellidae Kříž, 1965; = Hippomyidae Scarlato & Starobogatov, 1979; = Healeyidae Hautmann, 2008]

†Family CYPRICARDINIIDAE Ulrich, 1894

†Family HIPPOPODIUMIDAE Cox, 1969

†Family PALAEOPHARIDAE Marwick, 1953 [= Actinodontophoridae Newell, 1969]

†Family TUSAYANIDAE Scarlato & Starobogatov, 1979

†SPF KALENTEROIDEA Marwick, 1953¹¹³

†Family KALENTERIDAE Marwick, 1953 [= Pleurophoridae Dall, 1895 (invalid); = Myoconchidae Newell, 1957; = Permophoridae van de Poel, 1959]

¹¹⁰Molecular data (e.g., Taylor et al., 2009) place Solenoidea in a clade with Hiatellidae.¹¹¹Subfamily content following Cosel (1990, 1993), with nomenclatural adjustments herein.¹¹²Composition of Modiomorphoidea by JC. Modiomorphidae has priority over simultaneously published Palanatinidae following First Reviser action of Carter, herein; see Nomenclator.¹¹³Composition proposed by JC.¹⁰⁹Xylophagidae Purchon, 1941 is a junior homonym of Xylophagidae Fallén, 1810, based on *Xylophagus* Meigen, 1803 [Diptera] (see Nomenclator). An application will be presented to the ICZN to emend the junior bivalve name under Art. 55.3.1.

SPF GASTROCHAENOIDEA Gray, 1840

Family GASTROCHAENIDAE Gray, 1840 [= Chaeni-nae Gray, 1858; = Rocellariidae Ridewood, 1903; = Edentuloidea Cossmann, 1909 (n.a.)]

Order Pholadomyida Newell, 1965 [= Anomalodesmata Dall, 1889]**SPF uncertain:**

†Family UCUMARIIDAE Sánchez, 2003

SPF CERATOMYOIDEA Arkell, 1934

†Family CERATOMYIDAE Arkell, 1934 [= Ceromyi-daé Récluz, 1869 (invalid); = Myopholadidae Cox, 1964]

SPF CLAVAGELLOIDEA d'Orbigny, 1844¹¹⁴

Family CLAVAGELLIDAE d'Orbigny, 1844 (*nomen protectum*) [= Aspergillidae Burmeister, 1837 (*nomen oblitum*); = Humphreyiidae Gray, 1858; = Bryopinae Tryon, 1862; = Brechiti-nae Stoliczka, 1870; = Ensiphonacea Dall, 1889 (n.a.)]

Family PENICILLIDAE Gray, 1858

†SPF EDMONDIOIDEA King, 1850¹¹⁵

†Family EDMONDIIDAE King, 1850 [= Cardiomor-phidae S. A. Miller, 1877; = Allorismatidae Beurlen, 1954]

†Family PACHYDOMIDAE P. Fischer, 1887 [= Megadesmidae H. A. Vokes, 1967; = Astartilinae Waterhouse, 1969; = Ferraziidae Scarlato & Starobogatov, 1979; = Plesiocyprinellinae Simões, Marques, de Mello & Anelli, 1997]

¹¹⁴ Evidence now suggests that the Clavagellidae and Penicillidae were derived (Carter, 1978), perhaps independently (B. Morton, 2007, 2009), from the Lyonsiidae, bringing into question the superfamily Clavagelloidea.

¹¹⁵ Composition of Edmondioidea after Morris et al. (1991), except for present use of Pachydomidae instead of Megadesmidae.

SPF MYOCHAMOIDEA P. P. Carpenter, 1861

Family MYOCHAMIDAE P. P. Carpenter, 1861

Family CLEIDOTHAERIDAE Hedley, 1918 (1870) [= Chamostreidae Stoliczka, 1870]

SPF PANDOROIDEA Rafinesque, 1815

Family PANDORIDAE Rafinesque, 1815

Family LYONSIIDAE P. Fischer, 1887 [= Spinolyon-siellidae Scarlato & Starobogatov, 1983]

SPF PHOLADOMYOIDEA King, 1844¹¹⁶

Family PHOLADOMYIDAE King, 1844 [= Arcomyi-dae P. Fischer, 1887]

†Family BURMESIIDAE Healey, 1908

?†Family CERATOMYOPSIDAE Cox, 1964

†Family GRAMMYSIIDAE S. A. Miller, 1877
SF GRAMMYSIINAE S. A. Miller, 1877
SF CUNEAMYINAE Morris, Dickins & Astafieva-Urbajtis, 1991 [= ?Protomyidae Neumayr, 1891]¹¹⁷

†Family MARGARITARIIDAE H. A. Vokes, 1964

Family PARILIMYIDAE Morton, 1981

†Family PLEUROMYIDAE Zittel, 1895

†Family SANGUINOLITIDAE S. A. Miller, 1877
SF SANGUINOLITINAE S. A. Miller, 1877 [= Elymellidae Ulrich, 1894]
SF ALULINAE Morris, Dickins & Astafieva-Ur-bajtis, 1991
SF CHAENOMYINAE Waterhouse, 1966
SF PHOLADELLINAE S. A. Miller, 1877
SF UNDULOMYINAE Astafieva-Urbajtis, 1983
SF VACUNELLINAE Astafieva-Urbajtis, 1973 [= Myoniidae Scarlato & Starobogatov, 1979]

¹¹⁶ Composition of Pholadomyoidea largely following Newell (1969: N818) as modified by Runnegar (1974) and Morris et al. (1991), with additions by JC.

¹¹⁷ Morris et al. (1991) only tentatively placed *Proto-myia* in Cuneamyinae.

SPF THRACIOIDEA Stoliczka, 1870 (1839)¹¹⁸

Family THRACIIDAE Stoliczka, 1870 (1839) [= Osteodesmatidae Couthouy, 1839¹¹⁹; = Asthenothenaerinae P. Fischer, 1887]

Family LATERNULIDAE Hedley, 1918 (1840) [= Anatinidae Gray, 1840 (invalid)]

Family PERIPLOMATIDAE Dall, 1895

Clade Septibranchia (within Pholadomyida)**SPF CUSPIDARIOIDEA Dall, 1886¹²⁰**

Family CUSPIDARIIDAE Dall, 1886 [= Neaeridae Hidalgo, 1916 (invalid); = Cardiomyidae Scarlato & Starobogatov, 1983; = Myoneridae Scarlato & Starobogatov, 1983]

Family HALONYMPHIDAE Scarlato & Starobogatov, 1983

Family PROTOCUSPIDARIIDAE Scarlato & Starobogatov, 1983

?Family SPHENIOPSIDAE J. Gardner, 1928¹²¹

¹¹⁸The extant Pholadomyida/anomalodesmatan groups are here shown largely in their traditional arrangement. Harper et al. (2006) redistributed most families traditionally assigned to Thracioidea and Pandoroidea into "thraciid" and "lyonsiid" lineages, an action supported by sperm ultrastructure data (Healy et al., 2008). Data were insufficient for placement of Periplomatidae and more information is needed for a formal taxonomic rearrangement.

¹¹⁹Thraciidae is in prevailing usage and is conserved under ICZN Art. 40.2; see Nomenclator.

¹²⁰Classification following Krylova (pers. com., 9 September 2009).

¹²¹Placed by Marshall (2002: 271–284) in the Anomalodesmata on the basis of an internal ligament and a lithodesma, and in the Cuspidarioidea on the basis of commarginal sculpture. Membership in the Thracioidea might be as likely, and clearly this family would profit from molecular analysis.

SPF POROMYOIDEA Dall, 1886¹²²

Family POROMYIDAE Dall, 1886 [= Dermatomyidae Scarlato & Starobogatov, 1983; = Neaeroporomyidae Scarlato & Starobogatov, 1983; = Perlaporomyidae Scarlato & Starobogatov, 1983; = Cetomyinae Krylova, 1997]

Family CETOCONCHIDAE Ridewood, 1903

SPF VERTICORDIOIDEA Stoliczka, 1870

Family VERTICORDIIDAE Stoliczka, 1870

Family EUCIROIDAE Dall, 1895

Family LYONSIELLIDAE Dall, 1895 [= Policordiidae Scarlato, 1981; = Dallicordiidae Scarlato & Starobogatov, 1983]

†Order Orthonotida Pojeta, 1978**†SPF ORTHONOTOIDEA S. A. Miller, 1877**

†Family ORTHONOTIDAE S. A. Miller, 1877

†Family KONDURIIDAE Sánchez, 2007

?†Family PROTHYRIDAE S. A. Miller, 1889 [= Citothyrisidae Hajkr, Lukasová, Růžicka & Řehoř, 1974]

†Family SOLENOMORPHIDAE Cockerell, 1915
SF SOLENOMORPHINAE Cockerell, 1915 [= Solenopsidae Neumayr, 1891 (invalid)]
SF PROMACRINAE Scarlato & Starobogatov, 1979

¹²²Classification following Krylova (pers. com., 9 September 2009).

Notes added in proof:

The fossil family Rzehakiidae Korobkov, 1954, placed in the current classification within Veneridae (p. 130) should instead be listed under Solenoidea (p. 131), following Goncharova (1987).

The fossil family Manticulidae Waterhouse, 2008, placed in the current classification within Ambonychioidea (p. 118) should instead be listed under Buchioidea (p. 120), following JC (herein).

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Volume 2			
16	1–28	61–64	September 1854
17	29–60	65–68	October 1854
18	61–92	69–72	November 1854
19	93–124	73–76	January 1855
20	125–156	77–80	February 1855
21	157–188	81–84	April 1855
22	189–220	85–88	June 1855
23	221–252	89–92	September 1855
24	253–284	93–96	November 1855
25	285–316	97–100	March 1856
26	317–348	101–104	June 1856
27	349–380	105–108	August 1856
28	381–412	109–112	November 1856
29	413–444	113–116	March 1857
30	445–476	117–120	April 1857
31	477–508	121–124	September 1857
32	509–540	125–128	December 1857
33	541–572	129–132	January 1858
34	573–604	133–136	May 1858
35–36	605–660	137–138	November 1858

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Fascicule	Pages	Plates	Date
1	1–96	13–15	May 1880
2	97–387, title page		May 1881

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14	1–24	1–6	November 1887
15	25–60	7–11	August 1888
16	61–112	12–21	May 1889
17	113–172	22–29	April 1890
18	173–220	30–37	April 1891
19	221–272	38–44	April 1892
20	273–320	45–51	May 1892
21	321–388	52–59	November 1893
22	389–450	60–67	December 1893
23	453–540	68–78	March 1895
24	541–620	79–88	April 1896
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	xxv–xlvii	13 April 1822

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6	513–608	20 December 1883
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	15	81–120	Q, 41, 43, 44	March 1, 1849
	16	121–160	S, 45–47	April 2, 1849
	17	161–200	U, 42, 48, 49	May 1, 1849
	18	201–240	50–53	June 1, 1849
	19	241–280	AA, 54–56	July 2, 1849
	20	281–320	BB, 58, 59, 61	Aug. 1, 1849
	21	321–360	NN, 57, 62, 63	Sept. 1, 1849
	22	361–400	DD, 64–66	Oct. 1, 1849
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Palaeontology of New-York	Vol. 2	containing descriptions of the organic remains of the lower middle division of the New-York system (equivalent in part to the middle Silurian rocks of Europe)	i–viii, 1–362	1–85	Sept. 1852	Albany: van Benthuyssen
Geological Survey of New York	Vol. 3	containing descriptions and figures of the organic remains of the lower Helderberg Group and the Oriskany sandstone. 1855–1859				Albany: van Benthuyssen
Palaeontology	Part 1	[Text]	i–xii, 1–533		Sept. 1859	
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Geological Survey of the State of New York	Vol. 5 Part 2	[Text] containing descriptions of the Gasteropoda, Pteropoda and Cephalopoda of the upper Helderberg, Hamilton, Portage and Chemung Groups	i–xv, 1–492		Dec. 1879	Albany: van Benthuyssen & Sons
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	361–488	18 April 1847
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1	1	1–40	1–10	Nov. 1876
	2	41–64	11–20	Nov.–Dec. 1877
	3	65–88	21–30	Feb.–March 1878
	4	89–104	31–40	May 1878
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Livraison	Pages	Plates	Date
1		1–2	15 May 1835
3		4	15 May 1835
4		3	before 31 Aug. 1835
5		5–7	31 August 1835
6	1–48	10, 12	14 September 1835
7	49–72		23 November 1835
8	73–104		7 December 1835
9	105–128	9, 11, 13	4 January 1836
11	129–152	17, 21	18 April 1836
12	153–176	8	30 May 1836
13		18, 19, 22	-
14		20, 25	11 July 1836
15		23	1 August 1836
16		15, 16	26 September 1836
17	177–184	27, 28	3 October 1836
18		14, 26	7 November 1836
21		31	-
22		24, 35	27 February 1837
23		30, 32, 34	3 April 1837
24		35, 37	5 June 1837
25		38, 41	19 June 1837

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Livraison	Pages	Plates	Date
26		38, 39	7 August 1837
27		40, 45	18 September 1837
28		29, 46	-
29		41, 42, 43	6 November 1837
31	185–232	44	5 March 1838
32	233–280	47	23 April 1838
33	281–328	48, 52	6 May 1838
34	329–376		11 June 1838
35		49, 50, 51	11 October 1838
36		55	12 November 1838
37		56	8 April 1839
38		57	29 April 1839
39		58	24 June 1839
42		59	11 November 1839
43		64, 65	21 November 1839
44		54, 60–63	6 September 1841
46		66	8 November 1841
47		68, 69	8 November 1841
48		70	8 November 1841
49	377–408		15 November 1841
50		53, 67, 71	15 November 1841
51	409–424	72	15 November 1841
52	425–472	73, 74, 79	15 November 1841
53	473–488	75, 76, 80	14 February 1842
82	489–528		wrapper date 1846
83	529–600		wrapper date 1845
84	601–656		wrapper date 1846
85	657–704		wrapper date 1846
86	705–728		wrapper date 1846
?	729–758		?
88		83, 85	wrapper date 1842
89		78, 81	wrapper date 1847
90		79, 82	wrapper date 1847

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Livraison	Pages	Plates	Date
9		1	July 1836
14		2	December 1836
41	1–24		August 1839
42	25–48		September 1839
43	49–72		October 1839
45	73–104		January 1840
46	105–[136]		March 1840
49		4–5	June 1840
62		7	May 1842
63		3	May 1842
65		6, 7B	August 1842

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77–90	97–288	1844
91–102	289–448	1845
103–106	449–480	1846
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III, The Pelecypoda	1–4	1–222 (incl. 8α–δ)	1–12	1 September 1870	Trübner & Co.
	5–8	223–409	13–28	1 March 1871	
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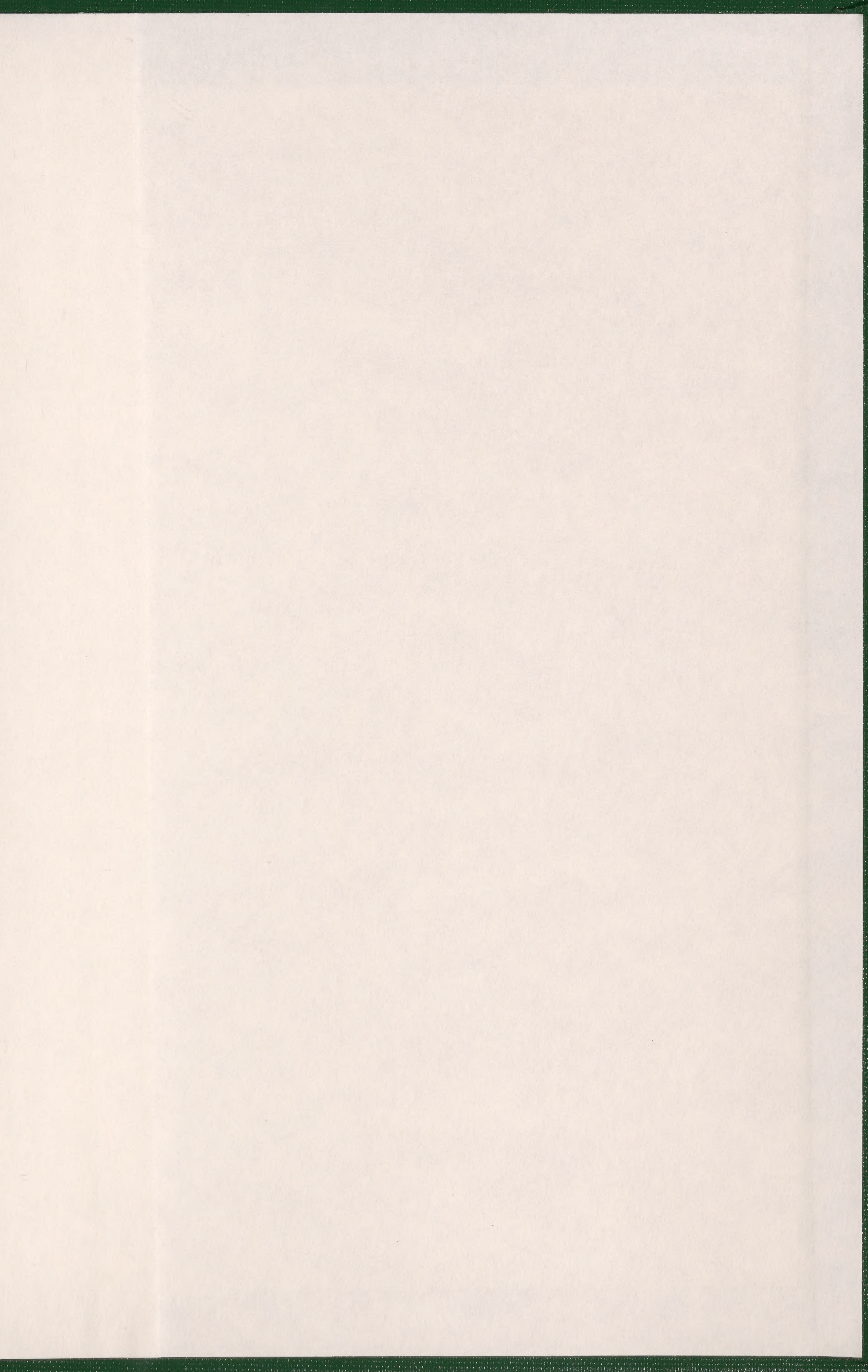
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